ECOLOGICAL AND PHYSIOLOGICAL ADAPTATIONS OF THE PORCUPINE TO WINTER IN ALASKA

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A

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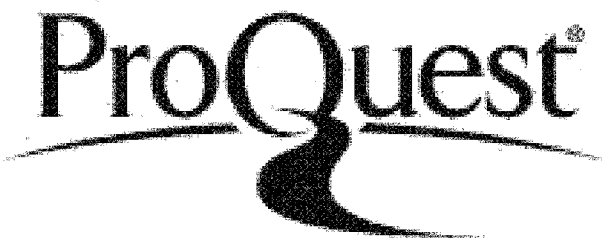

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ABSTRACT

Understanding the ecology and physiology of wildlife is paramount to conservation and management of species. North American porcupines (*Erethizon dorsatum*) are mammalian herbivores that occupy a diverse array of habitats across a broad geographical range. However, few studies have explored the ecology and physiology of porcupines. I used captive and free ranging porcupines to 1) identify the physiological abilities that enable them to survive on low quality winter forage when thermoregulatory demands are high, 2) determine responses of porcupines to winter conditions, and 3) determine how winter conditions influence habitat selection and home range size at the northern limits of their range.

My research revealed that the persistence of porcupines at the northern limits of their range is due to plasticity of food intake, as well as physiological tolerance of low-quality diets and low ambient temperatures. Captive porcupines gained mass when high quality diets were available. However, porcupines decreased their dry matter intake throughout winter, indicating a seasonal decrease in metabolic rate. Low requirements for energy and nitrogen minimized the loss of body mass when intakes were low, while plant toxins increased urinary losses of energy and nitrogen. Free-ranging porcupines conserved lean body mass in winter by catabolizing fat stores. Proportional fat loss was correlated positively with total fat mass at the start of winter. Fat losses were minimized by lowering rates of energy expenditure. Water turnovers were slow in wild porcupines and body temperatures were not reduced to save energy. In order to survive winter on a low quality diet of white spruce (*Picea glauca*) needles and cambium and paper birch (*Betula papyrifera*) cambium, porcupines maintained large home ranges comprised primarily of mixed conifer/hardwood forests. Occupying a mixed forest habitat allowed porcupine to switch their diet between two forage tree species, potentially alleviating saturated detoxification pathways. Overall, porcupines possess the physiological abilities of a specialist herbivore during winter; however, they rely on abundant high quality

summer forages to replenish their stores of fat and protein for reproduction and survival in the subsequent winter.

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CHAPTER 1 – INTRODUCTION: REDEFINING THE NORTH AMERICAN PORCUPINE (*ERETHIZON DORSATUM*) AS A FACULTATIVE SPECIALIST HERBIVORE[a]

Abstract

Herbivores have traditionally been categorized as either generalists or specialists based on either what they eat or what they are capable of eating due to physiological or morphological adaptations. However, recent literature argues that specialization should be based also on the limitations imposed on an animal by genetics and behavior. These authors categorize herbivores along a specialist-generalist continuum, with specialists defined as facultative or obligatory, based on seasonal or regional niche breadth. The North American porcupine, *Erethizon dorsatum*, has traditionally been categorized as a generalist herbivore. However, porcupines often function as dietary specialists consuming a difficult diet seasonally, regionally, or individually. Porcupines possess physiological and morphological adaptations to consume difficult diets and consume these diets at a higher rate compared to other herbivores. Therefore, porcupines should be reclassified as facultative specialists. However, additional research is required to better understand the degree of specialization exhibited by porcupines throughout their range. Comparative studies of diet selection across habitats will provide insight into regional and seasonal dietary specialization, and captive studies are required to understand the physiological mechanisms used by porcupines to consume difficult foods. Documenting inter-population and individual differences in the ability to metabolize plant secondary metabolites will provide insight into the ecology and evolution of porcupines, and will assist in managing potential impacts of porcupines on native flora as they expand into new habitats. Furthermore, determining variations in diet selectivity will promote cost effective management of porcupines as forestry pests.

[a]Coltrane, J. A. Redefining the North American porcupine (Erethizon dorsatum) as a facultative specialist herbivore. Wildlife Society Bulletin: *in review.*

Introduction

According to optimal foraging theory, herbivores will maximize their foraging efficiency by consuming the most profitable food sources while minimizing the associated costs of obtaining them (Charnov 1976, Stephens and Krebs 1986). Because plants vary in nutritional quality, as well as chemical and structural defense, herbivores must make foraging decisions that maximize their capacity to respond to such variation (Villalba et al. 2002). As a result, herbivores have developed specific feeding strategies to exploit food resources (Freeland 1991), and isotopic evidence suggests that changes in feeding strategies result in part from ecological responses to changes in the physical habitat (Cordon et al. 2008).

Ecologists have placed herbivores in dietary categories based on either what they eat or what they are capable of eating due to physiological or morphological adaptations. Traditionally, herbivores that consume a narrow diet (i.e. one to two plant species) have been classified as specialists (Crawley 1983), while those that exploit a wide array of food sources have been referred to as generalists. More recently, the definition of a specialist has focused on the ability of a herbivore to consume a "difficult" diet (Robinson and Wilson 1998), which is a diet not commonly used by other herbivores due to chemical or physical characteristics.

Shipley et al. (2009) argue that both descriptions are problematic in defining dietary specialization, and specialization should be based not only on an animal's interaction with food resources, but also on the limitations imposed on an animal by genetics, physiology, and behavior. They use the concepts of a fundamental niche, available diet, realized niche, and realized diet to categorize herbivores along a specialist-generalist continuum (Shipley et al. 2009). According to Shipley et al. (2009), a specialist is an herbivore that: 1) consumes difficult food, 2) has physiological or morphological adaptations that enable it to overcome the challenges of a difficult diet, and 3) consumes the difficult diet at a higher portion than other herbivores that have the same access to the food source. In addition, Shipley et al. (2009) distinguish between

"obligatory" and "facultative" specialists, because the degree of specialization can differ depending on seasonal and or regional variations in available diets. An obligatory specialist is an herbivore which always has a narrow realized niche; its diet is restricted by its ability to process a narrow range of difficult foods (Shipley et al. 2009). For example, while an obligatory specialist possesses the metabolic pathway to process specific plant secondary metabolites (PSM) found in one plant very well, it may not have additional pathways to process other PSM found in other plants, restricting its diet to just one or two plant species. A facultative specialist also has the ability to consume a difficult diet when the niche is restricted by season or by habitat (Shipley et al. 2009). Unlike the obligatory specialist, the facultative specialist also has the ability to consume a wide array of plant species that are not chemically or architecturally difficult when not limited spatially or temporally.

Regardless of definition, dietary specialization is rare in mammalian herbivores (Freeland and Janzen 1974, Crawley 1983, Freeland 1991, Shipley et al. 2009). The paucity of which has been explained by two prevailing theories: the Nutrient Constraint Theory (Westoby 1978) and the Detoxification Limitation Hypothesis (Freeland and Janzen 1974). The Nutrient Constraint Theory argues that a plant species cannot satisfy all the nutrient demands of a mammalian herbivore (Westoby 1978), while the Detoxification Limitation Hypothesis reasons that mammalian herbivores are incapable of detoxifying large amounts of chemically similar PSM (Freeland and Janzen 1974). Both theories provide cases for the prevalence of generalist herbivores, as few species exist that can either obtain all nutritional requirements from a single plant (Westoby 1978) or possess the ability to rapidly detoxify and eliminate similar PSM, thus reducing concentrations in the blood (Freeland and Janzen 1974).

The North American porcupine, *Erethizon dorsatum*, has traditionally been categorized as a generalist herbivore (Woods 1973) that consumes a wide array of plant species in a variety of habitats throughout North America (Roze 2009). However, seasonal or regional ecological limitations can restrict habitat and forage available to

porcupines (Roze 1984, Sweitzer and Berger 1992, Griesemer et al. 1998, Roze 2009). For example, low quality winter diets constrain porcupines at the northern reaches of their range (Griesemer et al. 1998, Roze 2009, Coltrane and Barboza 2010; **CHAPTER 2**), while predation may restrict foraging activity among individual porcupines in the southern parts of the range (Sweitzer and Berger 1992). This paper seeks to reclassify the North American porcupine as a facultative specialist (Shipley et al. 2009), that temporally or regionally consumes difficult food items that are unavailable to other mammalian herbivores. Its adaptability as a facultative specialist allows the porcupine to exploit a variety of habitats across a broad geographical range, unlike most North American mammalian herbivores.

Determining Dietary Specialization in Porcupines

Consuming a Difficult Diet

According to Shipley et al. (2009), the first requirement of a specialist herbivore is the ability to consume a difficult diet, generally defined as a diet which possesses chemical or physical properties that makes it inaccessible to most herbivores (Robinson and Wilson 1998). Seasonal variation in porcupine diet is apparent throughout most of their range (Dodge 1982, Roze 1984, Habeck 1990, Sweitzer 1996, Roze 2009). In winter porcupines primarily feed on the inner vascular tissue and coniferous needles of local tree species (Dodge 1982, Habeck 1990, Roze 2009, Coltrane and Barboza 2010); however, selection of forage species varies among regions and habitats (Tenneson and Oring 1985, Roze 2009). Regardless, winter diets are both physically and chemically defended, which makes them unobtainable or unpalatable to most other herbivores. To reach the inner vascular tissue of trees, porcupines must first remove the outer tree bark (Roze 2009). The outer bark of conifers is particularly thick, while conifer leaves are heavily coated in cuticular waxes, which presents a challenge to digestion by many herbivores. The presence of tannins, terpenes, and other phenolic compounds further add to the difficult nature of the winter diet (Tenneson and Oring 1985, Habeck 1990, Roze

2009, Coltrane and Barboza 2010; **CHAPTER 2**). In addition, most inner tree bark tissue is remarkably deficient in essential nutrients, such as nitrogen (Fournier and Thomas 1997, Felicetti et al. 2000, Roze 2009, Coltrane and Barboza 2010; **CHAPTER 2**; **CHAPTER 4**), making it a low quality forage.

Physiological and Morphological Adaptations for a Difficult Diet

The second requirement of a specialist herbivore is to possess morphological or physiological adaptations that allow the herbivore to consume a difficult diet (Shipley et al. 2009). Porcupines are physically well adapted to an arboreal lifestyle, which allows them to access their winter diet of tree bark and leaves. Long claws on their front and hind feet allow porcupines to grasp crevices of tree bark and propel themselves upward into the canopy and traverse narrow branches. Textured pads on the soles of their feet provide a rough surface to adhere to smooth bark of some trees, while heavily muscled hind limbs grasp the bole of smaller trees (Roze 2009). The porcupine's tail is also remarkably adapted to climbing. Bristles on the underside of the heavily muscled tail keep the porcupine from sliding backwards down the trunk of the tree as it uses its claws to propel it upward. Porcupines can also use their tails as braces while feeding on the trunk or branches of trees (Roze 2009).

The architecture of the porcupine's digestive system is well suited to break down and process tree leaves and bark, a trait which is only shared with a few species of North American rodents, including wood rats (*Neotoma spp.*; Dearing et al. 2005) and tree voles (*Aborimus spp.*). Four chisel-like incisors are used to scrape bark and nip twigs, while four premolars and twelve molars grind the vegetation into a fine pulp with a front to back motion (Dodge 1982). Porcupine incisors are located in the outside chamber of a two chambered mouth and are visible at all times, while the premolars and molars are contained behind interior lips. This double chambered design allows the porcupine to scrape bark from trees without opening its mouth, potentially reducing the loss of respiratory water and heat at low ambient temperatures. The digestive tract of the porcupine is large, up to 26 % of total wet body mass (Roze 2009). The cecum or

fermentation region is larger than predicted for their body size (Hume 1982, Vispo and Hume 1995, Felicetti et al. 2000), which allows porcupines to digest plant fibers at a rate that is higher than expected for medium-sized (<20 kg) herbivores.

Porcupines are able to consume winter diets low in nitrogen and energy and high in PSM and fiber by maintaining low daily requirements for energy (398 kJ · $kg^{-0.75}$ · d^{-1}) and nitrogen (209 mg · $kg^{-0.75}$ · d^{-1}) and by relying on body fat reserves to endure winter (Coltrane et al. 2011; **CHAPTER 3**). However, the metabolic pathways employed by porcupines to deal with various PSM are yet unknown. Roze (2009) hypothesized that porcupines practice geophagy, possibly to deal with PSM in their diet. Ingested clay binds with plant tannins (Johns and Duquette 1991), reducing the metabolic costs associated with producing tannin-binding salivary proteins. Although clay consumption is often related to sodium deficiencies, Roze (2009) observed that fecal clay content of wild porcupines did not correspond to periods of sodium deficiency, therefore further supporting the Detoxification Limitation Hypothesis.

Consumption Rate of Difficult Diet in Relation to Other Herbivores

The porcupine's arboreal lifestyle and winter diet reduces resource competition with other mammalian herbivores, although few studies have directly measured this potential interspecific competition (Habeck 1990). Regardless, competition for forage most likely varies among habitats and regions. In the front range of Colorado porcupines displayed significantly different feeding patterns than those of Albert's squirrels (*Sciurus aberti*), an arboreal herbivore that occupies overlapping habitat (Habeck 1990). During winter porcupines targeted Ponderosa pine trees (*Pinus ponderosa*) at a higher rate than the squirrels.

Porcupines as Facultative Specialists

Seasonal Specialization

Specialist herbivores may have evolved with the few plants that comprise their diet, and as a result, possess only those metabolic pathways to cope with the specific

PSM found in these target species (Freeland and Janzen 1974, McArthur et al. 1991, Marsh et al. 2003, Sorensen and Dearing 2003, Sorensen et al. 2004). Obligatory specialists are typically incapable of broadening their diet breadth to include other plant species that may contain different PSM (Moore and Foley 2005, Shipley et al. 2009). Diet switching among seasons can be physiologically challenging, and seasonal dietary specialization has been documented in only a few mammalian herbivores (Shipley et al. 2006). One facultative specialist that displays seasonal dietary selection is the pygmy rabbit (*Brachylagus idahoensis*). In the winter, the pygmy rabbit consumes a diet that is 99% big sagebrush (*Artemisia tridentate*), a plant heavily defended with monoterpenes and other PSM, while in the summer, pygmy rabbits forage on a varied diet that is only 50% big sagebrush (Green and Flinders 1980, Thines et al. 2004). Pygmy rabbits are not obligated to eat only sagebrush and will chose a higher quality diet when available; thus, pygmy rabbits possess a large fundamental niche. However, maintaining seasonal variation in diet does have costs. While pygmy rabbits are able to meet nutritional requirements on a diet dominated by sagebrush, they require high daily energy intakes to offset the cost of metabolizing PSM (Shipley et al. 2006). Increased metabolic costs associated with detoxification of PSM should arguably be higher in facultative specialists than in obligatory specialists, because facultative specialists typically function as generalist herbivores at some point during the year (Sorensen et al. 2004).

Porcupines exhibit seasonal diet variation throughout much of their range (Shapiro 1949, Griesemer et al. 1998, Roze 2009); however, seasonal diet specialization has been documented in only a few populations during winter (Shapiro 1949, Griesemer et al. 1994, Griesemer et al. 1998). For example, porcupines in central Massachusetts used hemlock trees (*Tsuga Canadensis*) 71-80 % of the time even though hemlocks comprised only 6 % of the available trees. Similar diet selection was observed by porcupines in the Adirondacks (Shapiro 1949).

In the mixed deciduous-coniferous forests of southcentral Alaska, porcupines forage on white spruce (*Picea glauca*) needles and the inner vascular tissues of white

spruce and paper birch (*Betula papyrifera*) during winter (**CHAPTER 4**). However, like the pygmy rabbit, porcupines pay high energetic costs for their winter diet. While captive porcupines digested 87–92 % of phenols ingested with white spruce needles, digestible phenol intake accounted for 64% of the variation in urinary energy loss compared to porcupines fed a formulated diet free of PSM (Coltrane and Barboza 2010; **CHAPTER 2**). These results suggest that porcupines accrue a high energetic cost when metabolizing certain PSM, similar to other facultative specialists. Furthermore, porcupines must offset this cost by catabolizing fat reserves and rely on the emergence of spring forage and the corresponding diet change to higher quality forage to survive (Coltrane et al. 2011; **CHAPTER 3**).

Individual Specialization

Wide diet breadth that characterizes the species as a whole is not always realized at the individual level. Dietary specialization can vary locally among groups and individuals of the same species (Mangione et al. 2000, Bolnick et al. 2003, Degabriel et al. 2009) and has been attributed to local variation in habitat (Roze 1984, McEachern et al. 2006, de Souto Lima et al. 2010) and varying levels of predation risk (Sweitzer and Berger 1992). However, some evidence suggests that individuals can adapt physiologically to local dietary specialization over time (Bolnick et al. 2003, McEachern et al. 2006, Cordon et al. 2008, Degabriel et al. 2009). For example, dusky-footed woodrats (*Neotoma fuscipes*) have local dietary specialization even though they are considered a dietary generalist that uses a wide variety of plant communities. Cafeteria trials revealed that individual woodrats avoided consuming plants that were preferred by woodrats from neighboring habitats. Individuals avoided novel plants with high levels of PSM and selected familiar plants that were chemically-defended. These data suggest that induced preferences for toxic plants may be indicative of underlying adaptations to PSM that could promote additional behavioral, physiological, and ultimately genetic differences between individuals in different habitats (McEachern et al. 2006). Similarly, Degabriel et al. (2009) concluded that dietary variation among populations of brushtail

possums (*Trichosurus vulpecula*) may have resulted in local variations in physiological abilities to cope with PSM.

Individual variations in diet selection have been observed in both North American porcupines (Roze 1984, Tenneson and Oring 1985, Roze 2009), as well as their South American relative, the thin spined porcupine (*Chaetomys subspinosus*; de Souto Lima et al. 2010). The thin spined porcupine is found throughout forested regions of Brazil and is considered a generalist herbivore which consumes up to 14 species of plants; however, individual porcupines specialize on the leaves of up to three species (de Souto Lima et al. 2010). Like the woodrat, thin spined porcupines might be considered a generalist at the population level, but they appear to be facultative specialists at the individual level.

A similar argument for individual specialization can be made for North American porcupines. One of the most detailed records of individual diet variation has been documented for porcupines in the Catskill Mountains (Roze 1984; 2009). During winter, porcupines fed exclusively on the inner vascular tissue of ten species of trees; however, beech (*Fagus grandifolius*) and sugar maple (*Acer sacarum*) were preferred, and individual porcupines specialized on only one to two species of trees all winter. The primary food choice of individuals was directly related to the density of that tree within the individual's feeding area; however, this was not the case for the secondary food choice (Roze 1984). Further evidence for individual specialization is provided by observations of two groups of porcupines in Itasca State Park, Michigan that were separated by 3 km (Tenneson and Oring 1985). In one area, 90 % of the porcupine winter diet was white pine (*Pinus strobus*), elm (*Ulmus americana*), and linden (*Tilia americana*); whereas these species only comprised 23 % of the diet of the second group. Furthermore in southcentral Alaska, individual variation in tree selection was significant in mixed coniferous/hardwood forests (**CHAPTER 4**).

While habitat has been implicated as the driving factor in most local individual specializations, predation may also play an important role in diet specialization. Habitat use varies depending on age class in the Great Basin Desert of Nevada (Sweitzer and

Berger 1992). Juvenile porcupines that are smaller bodied and less defended than adults, were typically found in densely vegetated buffalo-berry (*Shepardia argentia*) and willow (*Salix spp.*) groves. In comparison, adult porcupines (> 2-years-old) preferred higher quality forage in open groves and grasslands. This differentiation in habitat selection between adults and juveniles is speculated to be a direct response to predation risk and vulnerability to predation by the smaller bodied individuals (Sweitzer and Berger 1992).

Conclusions

While the porcupine is one of the most widespread rodents in North America (Dodge 1982), surprisingly few studies have explored the ecology and physiology of this adaptable species. Evidence suggests that while a generalist herbivore at the species level, the porcupine exhibits dietary specialization on a regional, temporal, and individual basis, and therefore fits into the category of facultative specialist described by Shipley et al. (2009). However, additional research is required to better understand the degree of specialization exhibited by porcupines throughout their range. Comparative studies of diet selection across habitats will provide insight into regional and seasonal dietary specialization. The use of stable isotope ratios have been used to reconstruct dietary niche-breadths in extinct and extant herbivores (Cordon et al. 2008), and may be useful in identifying seasonal dietary shifts in porcupines. Captive studies are required to understand the physiological mechanisms used by porcupines to consume difficult foods, specifically metabolic pathways used to process PSM found in local plants. Furthermore, documenting inter-population and individual differences in the ability to metabolize PSM will provide insight into the ecology and evolution of porcupines, which may ultimately explain habitat selection, dispersal and gene flow (Mangione et al. 2000) of porcupines.

Management Implications

Porcupines have been characterized as pests throughout most of their range, and as a result, research has often focused on the damage porcupines inflict on commercial

forestry operations (Krefting et al. 1964, Storm and Halvorson 1967, Tenneson and Oring 1985, Sullivan et al. 1986). Most studies have examined the effect of porcupine feeding on tree growth and survival or factors that contribute to forage selection by examining forage trees (Storm and Halvorson 1967, Sullivan et al. 1986), while few studies have focused on actual porcupine behavior (Tenneson and Oring 1985). An understanding of regional, individual and seasonal variation in porcupine diet is often absent, yet is paramount to designing effective management strategies to reduce porcupine damage. Removing individual porcupines that exhibit dietary selection which conflicts with forestry operations may ultimately be more cost effective than large scale removal efforts and yield the same management results.

The dietary versatility of the porcupine as a facultative specialist makes it an incredibly adaptable species, as demonstrated by both northward and southward range expansions (Spencer 1964, Payette 1987, Ilse and Hellgren 2001). Distributional changes may have significant impacts on ecosystems, especially on rare species (Alverson et al. 1988). For example, Ilse and Hellgren (2001) speculate that expansion of porcupines onto the Edwards Plateau of Texas may increase the susceptibility of paper-shell pinyon pine (*Pinus remota*) to pine engraver beetle (*Ips hoppingi*) infestation. Understanding the physiological and morphological ability of porcupines to specialize on novel diets will assist in predicting and therefore managing impacts as they occupy new habitats.

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CHAPTER 2 - WINTER AS A NUTRITIONAL BOTTLENECK FOR NORTH AMERICAN PORCUPINES (*ERETHIZON DORSATUM*)[a]

Abstract

North American porcupines are distributed across a wide variety of habitats where they consume many different species of plants. Winter is a nutritional bottleneck for northern populations, because porcupines remain active when environmental demands are high and food quality is low. We used captive porcupines to examine physiological responses to low quality diets at high energy demands during winter at ambient temperatures as low as -39 °C. We did not observe an endogenous pattern of body mass gain or loss when porcupines were fed a low nitrogen diet (1.1 % dry matter) ad libitum through winter. Dry matter intake declined from 43.6 to 14.6 $g \cdot kg^{-0.75} \cdot d^{-1}$ even though ambient temperatures declined from -3 °C to -30 °C, which indicates a seasonal decrease in metabolic rate. Porcupines consuming white spruce needles maintained digestive efficiency for energy (61 %) and neutral detergent fiber (50 %). However, low requirements for energy (398 $kJ \cdot kg^{-0.75} \cdot d^{-1}$) and nitrogen (209 $mg \cdot kg^{-0.75} \cdot d^{-1}$) minimized the loss of body mass when intakes were low and plant toxins increased urinary losses of energy and nitrogen. Porcupines were also able to tolerate low intakes of sodium, even when dietary potassium loads were high. Porcupines use a flexible strategy to survive winter: low requirements are combined with a high tolerance for dietary imbalances that minimize the use of body stores when demands exceed supply. However, body stores are rapidly restored when conditions allow. Porcupines possess many physiological abilities similar to specialist herbivores but retain the ability of a generalist to survive extreme conditions by using a variety of foods.

Introduction

Animals that can exploit a wide range of habitats may be able to tolerate extremes of environmental exposure and dramatic changes in food quality and abundance. North

[a]Coltrane, J. A. and P. S. Barboza. 2010. Winter as a nutritional bottleneck for North American porcupines (*Erethizon dorsatum*). Journal of Comparative Physiology, B: Biochemical, Systematic, and Environmental Physiology 180: 905-918

American porcupines (*Erethizon dorsatum*) are medium-sized (< 15 kg), generalist herbivores (Woods, 1973) found in a wide range of habitats from desert chaparral to temperate forests and arctic tundra. During winter, porcupines consume a low-quality diet, including woody plants that are low in nitrogen (N) and high in both fiber and plant secondary metabolites (PSM; Griesemer et al., 1998; Roze, 1984, 1989; Sweitzer, 1996; Tenneson and Oring, 1985). Consequently, porcupines typically lose body mass and have a high risk of winter mortality (Berteaux et al. 2005; Oveson, 1983; Roze, 1984; Smith, 1979; Sweitzer and Berger, 1993; Tenneson and Oring, 1985). As a result, winter is a nutritional bottleneck for porcupines at the northern limits of their distribution.

Alaska is the northern-most range of the North American porcupine. During an Alaskan winter, porcupines are exposed to low ambient air temperatures combined with deep snows and strong winds. In mixed deciduous and coniferous forests of Southcentral Alaska, the winter diet of porcupines is primarily cambium and needles of white spruce (*Picea glauca*), as well as cambium of paper birch (*Betula papyrifera*). The nutritional value of these foods is extremely low, as they are high in fiber and PSM, and very low in N (< 1 % dry matter) and sodium (Na). However, both white spruce and paper birch are readily available in these mixed forests, and therefore food abundance should not limit winter survival. Alaskan porcupines can be found foraging at ambient temperatures below -25 °C, which is significantly less than their reported lower critical temperatures of +10 °C (DeMatteo and Harlow, 1997) and -2 °C (Fournier and Thomas, 1999). Such activities should result in increased thermoregulatory costs, and therefore increased energy requirements.

The physiological ability of porcupines to extract energy and nutrients from a low quality diet is paramount to surviving the bottleneck of winter. In general, digestion of plant fiber by porcupines is higher than expected for medium-sized (< 15 kg) herbivores, because they retain fiber in a fermentation region that is larger than predicted for their body size (Felicetti et al., 2000; Hume, 1982; Vispo and Hume, 1995). To survive winter porcupines may be able to increase food intakes to maintain digestible supplies of energy and nutrients from fibrous forages. However, high levels of PSM may reduce the

nutritional value of a plant by depressing food intake or increasing the costs of energy, nutrients and water needed to process the toxic compounds (Dearing et al., 2000; Freeland and Janzen, 1974; Moore and Foley, 2005; Provenza et al., 2003; Sorensen et al., 2005). Processing secondary plant metabolites may also reduce foraging time or the duration of feeding bouts (Foley et al., 1999; Wiggins et al., 2006; Wiggins et al., 2003), resulting in an overall reduction of energy and nutrient intake (Sorensen et al., 2005).

We used captive porcupines to examine physiological responses to low quality diets at high energy demands during winter at ambient temperatures as low as -39 °C. We fed porcupines two diets that were low in N and high in fiber: a formulated diet low in PSM, and white spruce needles that were high in PSM, low in Na and high in potassium (K). We measured intake and excretion of energy substrates, N and minerals throughout winter from October to March to estimate requirements in relation to body mass changes and net retention of energy and nutrients.

Methods

Animals

We captured nine adult porcupines in Anchorage (n = 7; 61.17 N, 150.02 W) and Fairbanks (n = 2; 64.82 N, 147.87 W), Alaska. Porcupines were captured with dip nets or live traps and then transported to the Biological Reserve at University of Alaska Fairbanks (UAF). All individuals were determined to be adults (> 2 years) based on tooth eruption patterns and body mass (> 5 kg; Dodge, 1982). The Institutional Animal Care and Use Committee approved all procedures under UAF protocol #06-027.

Porcupines were housed in individual pens (1.22 m x 1.83 m x 2.44 m) equipped with climbing structures and a plastic den filled with straw. The pens were located outdoors under a roof in a wire and plywood enclosure, which was exposed to ambient temperatures, but protected from precipitation. Porcupines were provided with food and water or snow *ad libitum*. We used a pelleted formulation (Alaska Mill and Feed, Anchorage, Alaska) to mimic the low concentration of N and the high concentration of fiber in the natural winter diet while still maintaining concentrations of minerals and trace

nutrients that were adequate for other herbivores. Porcupines were trained to frequent handling for weighing and transfer between cages. We recorded body mass (± 0.01 kg, AE Adams CPW Plus 35, Adam Equipment Inc. Danbury, CT) each week and both before and after each experimental period. Ambient air temperatures were recorded every 0.5 h (HOBO Pro Series Temp, ONSET, Pocasset, Mass.) throughout the study.

Feeding Trials

We measured responses of porcupines in three periods during the winter of 2006-2007: early winter (October; n = 9), mid-winter (December; n = 7), and late winter (February; n = 7). All porcupines were fed the formulated diet (n = 9) in early winter, whereas responses to both diets were measured in mid-winter (n = 7) and late-winter (n = 7). We used a repeated measures design during mid-winter and late winter to evaluate the effects of diet (between animals) and period (within animals). During the mid- and late winter experimental periods, four porcupines were fed white spruce needles, and three porcupines were fed the formulated diet. Each experimental period consisted of three phases: diet adjustment (7-10 d), cage adjustment (4-7 d), and collection (5-7 d). Porcupines were adjusted to their designated diet in the large enclosures until daily intake ($g \cdot d^{-1}$) stabilized (CV = 12 %). We then transferred the porcupines to individual metabolic cages to allow sample collection when food intakes were stable.

Metabolism cages (0.91 m x 0.91 m x 0.91 m) were located in the same outdoor enclosure as their larger pens. Food and snow were offered *ad libitum*. The formulated diet was offered in a container secured to the side of the metabolic cage, whereas white spruce needles were offered on branches secured to the door of the cage. Food intake was measured daily by subtracting refused food from the amount of food offered the previous day (± 0.1 g, CT6000, Ohaus Corporation, Florham Park, NJ). The floor of each cage was a removable stainless steel grate (1.3 x 1.3 cm) over a collection tray. A wire mesh (0.6 x 0.6 cm) was placed over the tray to separate feces from urine. Urine flowed into the collection tray and then to a plastic collection bottle. Collected food and excreta were weighed (± 0.1 g), sub-sampled and frozen for storage each day. However,

urine froze in the collecting pan during the late winter collection period, and had to be thawed before daily sampling.

Blood was sampled at the end of the collection period in early-winter (October) and mid-winter (December) and then once again in April after the late-winter collection (February). Blood was drawn into a 3 ml syringe from the jugular vein with a 23 gauge x 2.5 cm needle and transferred to a 4.0 ml vacutainer tube that contained lithium heparin (BD, Franklin Lakes, NJ). Plasma was separated from red blood cells by centrifugation (3, 000 x *g* for 10 min) and frozen at -20 °C until analysis.

Chemical Analysis and Calculations

Daily samples of food and feces were dried at 55 °C in a fan-forced oven, whereas urine samples were freeze-dried (Freeze Dryer 8, Labconco Corporation, Kansas City, Mo) to a constant mass to determine dry matter (DM) content. Food and feces were ground through #20 (1.25 mm) screen in a Wiley Mill. White spruce needles were ground in the same manner but with dry ice (solid CO_2) to prevent separation of resins in the mill. Representative samples of food, feces or urine from each animal were prepared by combining a proportionate mass of sample from each day during each period.

Gross energy of urine, food, and feces was measured in an adiabatic bomb calorimeter (Parr Instruments, Boleen, IL). Total ash was determined by combusting samples in a muffle furnace (Thermolyne F62700, Barnstead Int., Dabuque, IA) at 500 °C for four hours. Organic matter was calculated as the difference between dry matter and total ash. We used an elemental analyzer (CNS2000, LECO, St. Joseph, MI) to determine N content, which was converted to organic matter in crude protein at 6.25 g organic matter$\cdot g^{-1}$ N in food and 14 g organic matter$\cdot g^{-1}$ N in feces (Robbins, 1993; Van Soest, 1994). Fiber was analyzed by detergent extraction (Van Soest et al., 1991) in polyester bags (F57 bags, Ankom, Macedon, NY). Neutral detergent fiber (NDF) was extracted with thermo-stable amylase (Ankom) to dissolve starches, and with sodium sulfite to denature structural proteins. The NDF residue of feces was analyzed for N to assess indigestible N loss. Acid detergent fiber (ADF) was extracted sequentially from

the neutral detergent residue of food and feces. We estimated non-structural carbohydrates and hemicelluloses by difference in mass between residues of the sample. Van Soest (1994) discussed the errors of this approach, which include uncertainty in measurement of both residues, as well as the variation in the specificity of the extractions among foods and between foods and feces. We assumed that the neutral detergent procedure dissolved crude protein, lipids and non-structural carbohydrates (e.g., sugars, starches, pectins). We therefore estimated non-structural carbohydrate (hereafter soluble carbohydrate) as organic matter minus NDF and crude protein. Our calculation assumed that lipid content was low because crude fat is less than 7 % of dry matter in the formulated diet and in most forages (Barboza and Parker, 2006; Van Soest, 1994). Furthermore, we assumed that most of the mineral ash was associated with cell contents, because ash in the ADF residue was only 8 ± 3 % of total ash in the formulated diet. Hemicelluloses were estimated as the difference between NDF and ADF residues by assuming that further dissolution of minerals in acid detergent was negligible.

Food and excreta were digested in a mixture of 70 % v/v HNO_3 (1000 mL), 32 *M* H_2SO_4 (200mL), 70 % v/v $HClO_4$ (343 mL), and water (57 mL) to remove all organic matter for mineral analysis. Digestions were performed in a sequence: 66 °C for 10 min, 107 °C for 10 min, 149 °C for 30 min, 204 °C for 30 min, and 260 °C for 30 min. Acid digests were diluted with distilled water and assayed by directly coupled plasma spectrometry (Iris DCP, Thermo Elemental, Cheshire, U.K.).

Total phenols were determined in both food and excreta using the method described by Singleton et al. (1999). Samples were first extracted with acetone, and then diluted with deionized water, Folin-Ciocalteau Reagent (Sigma-Aldrich Catalog # F9252-1L) and 20 % sodium carbonate solution. Absorbance was measured at 765 nm in a spectrophotometer (Beckman DU 530, Fullerton, CA). Total phenols were calculated as equivalents of gallic acid and reported as mmol·100 g DM^{-1}.

We calculated daily intakes of energy, organic components, and elements as the difference between total amounts offered and refused (Barboza et al., 2009). Rejected foods were contaminated with minerals from small amounts of excreta. We therefore

assumed that the composition and mineral content of the foods offered was equal to those of the foods refused. Digestible intakes were calculated as the apparent disappearance of each component from the diet when compared with feces. Metabolizable fractions were subsequently calculated by subtracting the urinary loss from digestible intake of each component (Barboza et al., 2009). For simplicity, we used "digestible intakes" and "digestibilities" to refer to "assimilated intakes" and "assimilation efficiencies" for both organic and inorganic components of the diet. Similarly, "metabolizable intakes" and "metabolizabilities" were used to describe the retention or balance of both inorganic and organic components of the diet. We used the N in NDF from feces to measure the loss of indigestible N because most of the soluble N in feces from herbivores is associated with microbes and unresorbed secretions (Mason, 1969; Van Soest, 1994). Metabolic fecal nitrogen (MFN) was therefore estimated by subtracting the N in fecal NDF from total N in feces (Barboza and Parker, 2006) with the assumption that true digestibility of N was high and similar between these diets.

Plasma and urine were thawed to room temperature for analysis. Osmolality was measured by vapor pressure (Vapro 5520, Wescor, Logan, Utah), and pH of urine samples was measured using a pH/ion meter (model 315, Corning, NY). Plasma was deproteinized with trichloroacetic acid (Peltier et al., 2003). Deproteinized plasma and urine were assayed for urea by the diacetyl monoxime method (Marsh et al., 1965).

Statistics were analysed with modules in SYSTAT 11 (SYSTAT Software, Richmond, Calif.). Repeated measures of daily intakes of energy, organic components, and elements were compared by ANOVA between diets and seasons (mid and late winter only) for individual porcupines (formulated diet: $n = 3$, white spruce needles: $n = 4$). Pair-wise contrasts were executed with Bonferroni's adjustments for multiple comparisons. Data expressed as proportions or percentages (e.g., digestibilities and metabolizabilities) were transformed to the arcsine of the square root for ANOVA (Zar, 1999). We used t-tests to compare diet compositions and to determine if means differed significantly from zero. Statistical significance was determined as $\alpha < 0.05$. Means are

reported with one standard deviation (± SD). Linear regressions are reported with the standard error of the estimate.

Results

Experimental Conditions

During experimental periods, average daily temperatures ranged from -3.45 ± 2.88 °C in early winter to -29.98 ± 4.83 °C in late winter. Day length was shortest in mid-winter (3.93 ± 0.08 $h \cdot d^{-1}$) but increased to 12.58 ± 0.17 $h \cdot d^{-1}$ in late winter (Figure 2.1A). Mean daily temperatures ($f = 60.77$, $p < 0.0001$) and day length ($f = 3214.22$, $p < 0.0001$) varied significantly among all collection periods (Figure 2.1A).

In comparison with the formulated diet, white spruce needles were lower in N, soluble carbohydrates, and Na, but higher in gross energy, NDF, ADF, total ash, total phenols, and calcium (Table 2.1). Variation in dietary components for each experimental diet was low among winter periods (Table 2.1).

Body Mass

Porcupines were maintained on the formulated diet between experimental periods throughout winter. Body mass did not change significantly over winter regardless of the diets fed during experimental periods (Figure 2.1B; $f = 0.60$, $p > 0.05$). Peak winter body mass was similar for porcupines fed white spruce needles and those fed the formulated diet. Peak winter body mass was attained by individuals from 17 October to 9 February at 6.45 to 12.56 kg (Figure 2.1B).

Body mass at the start of each experimental period did not differ between diets ($f = 0.09$, $p > 0.05$) or among early, mid-, and late winter collection periods ($f = 0.86$, $p > 0.05$). Porcupines fed the formulated ration maintained body mass during early and mid-winter collection periods, and only decreased body mass slightly during the late winter period (-30.6 ± 7.6 $g \cdot d^{-1}$; $f = 1.98$, $p > 0.05$). Porcupines fed white spruce needles experienced higher daily mass loss than those animals fed the formulated ration in mid- and late winter ($f = 10.95$, $p = 0.020$). Porcupines fed white spruce needles lost 52.5 ±

24.0 $g \cdot d^{-1}$ in mid-winter and 44.6 ± 16.4 $g \cdot d^{-1}$ in late winter, whereas porcupines fed the formulated ration maintained mass during mid-winter but lost 30.6 ± 7.6 $g \cdot d^{-1}$ during late winter.

Responses to Winter

Dry matter intake (DMI) of porcupines fed the formulated ration (n = 3) decreased through winter from 43.62 ± 12.73 $g \cdot kg^{-0.75} \cdot d^{-1}$ in early winter to only 14.58 ± 2.06 $g \cdot kg^{-0.75} \cdot d^{-1}$ in late winter ($f = 13.93$, $p = 0.02$; Figure 2.2). Intakes of digestible and metabolizable DM also decreased ($p < 0.02$) through winter, because digestibilities and metabolizabilities of DM did not change between periods ($p > 0.05$; Table 2.2). Similarly, digestible intakes of most dietary components (i.e., fiber fractions, energy, N and all minerals, except magnesium) also decreased from early to late winter ($p < 0.02$). Metabolizable energy intake decreased through winter from 546.05 ± 172.36 $kJ \cdot kg^{-0.75} \cdot d^{-1}$ in early winter to 252.64 ± 4.72 $kJ \cdot kg^{-0.75} \cdot d^{-1}$ in late winter ($f = 11.93$, $p = 0.02$). Conversely, metabolizable intake of N was similar between periods (0.123 ± 0.102 $g \cdot kg^{-0.75} \cdot d^{-1}$).

Dry matter digestibility was high for the formulated ration (70 – 75 %; Table 2.2) and did not differ among winter periods. Digestibilities of fiber, energy, N and most elements were not affected by the decrease in DMI or by the winter period ($p > 0.05$; Table 2.2). However, K intake decreased by 70 % from early to late winter ($f = 14.58$, $p = 0.015$; Figure 2.2); whereas, K digestibility increased by 20 % over the same time period ($f = 15.43$, $p = 0.013$; Figure 2.2), which maintained metabolizable intake of K through winter. Concurrently, metabolizabilities of organic matter, gross energy and all elements, including Na, did not change from early to late winter on the formulated diet ($p > 0.05$; Table 2.2).

Responses to Diet

Porcupines fed white spruce needles were 7-14 % less efficient in digesting DM ($p < 0.005$; Tables 2.2 – 2.4) than porcupines fed the formulated ration in mid- and late winter. Metabolizability of DM in mid-winter was higher in porcupines fed the natural

diet compared to the formulated diet ($p < 0.001$). Decreases in digestible DMI over the duration of the winter resulted in decreased digestibilities of DM from mid- to late winter (Table 2.3, 2.4).

Declines in digestible intakes of dietary components between mid- and late winter were less pronounced for porcupines fed the white spruce needles than for those fed the formulated diet. Digestible intakes of white spruce needles were higher than those of the formulated diet for both NDF and ADF during the experimental periods ($p < 0.005$; Table 2.4). Conversely, digestible intake of soluble carbohydrate from white spruce needles was lower than that of the formulated diet in both winter periods ($p < 0.05$; Table 2.4).

Digestible energy and N intakes decreased simultaneously with digestible DMI over the winter in both dietary groups ($p < 0.05$; Table 2.4). In addition, porcupines fed white spruce needles ingested less digestible N in mid- and late winter, respectively, when compared to porcupines fed the formulated diet ($p < 0.05$; Table 2.4).

Digestible intakes of minerals varied between diets and periods. White spruce needles contained low amounts of Na, which resulted in negligible digestible intake of Na by porcupines fed this diet during both winter periods (Table 2.1, 2.4). Conversely porcupines fed white spruce needles had a higher digestible Ca intake during both winter periods ($p = 0.023$; Table 2.3) compared to the formulated diet group.

Metabolizable DMI followed the same patterns of digestible DMI between diets and experimental periods (Table 2.4, 2.5). Although digestible intake of energy was similar between diets, metabolizable energy intake was 42 % lower in porcupines fed white spruce compared to the formulated diet in mid-winter ($p = 0.002$; Table 2.5). Metabolizable energy intake decreased seasonally in both groups, and to a greater extent for animals consuming white spruce needles (diet and period effect; $f = 9.93$, $p = 0.025$).

Phenol concentration in white spruce needles was 0.574 ± 0.008 mmol·g DM^{-1} compared to 0.0006 ± 0.003 mmol·g DM^{-1} in the formulated ration (Table 2.1). Consequently, digestible intakes of phenols were negligible on the formulated ration. In contrast, porcupines fed white spruce needles ingested 0.154 ± 0.005 mmol·g DM^{-1} and 0.110 ± 0.019 mmol·g DM^{-1} in mid- and late winter, respectively. Porcupines apparently

digested 87 to 92 % of phenols ingested with white spruce needles. Digestible phenol intake accounted for 64 % of the variation in urinary energy loss ($p = 0.018$; Figure 2.3). Dry matter content of urine and total urinary output of DM were greater for porcupines fed white spruce needles compared to those animals fed the pelleted ration (20 ± 6 % vs. 8 ± 3 %).

Metabolic Responses

The energy required to maintain body mass during winter was 398 ± 28 $kJ \cdot kg^{-0.75} \cdot d^{-1}$ for porcupines on both diets (Figure 2.4). Urinary energy loss was higher in porcupines fed white spruce compared to those fed the formulated ration. In mid-winter, porcupines lost 6.36 ± 2.84 $kJ \cdot kg^{-0.75} \cdot d^{-1}$ and 65.08 ± 11.42 $kJ \cdot kg^{-0.75} \cdot d^{-1}$ in urine when eating formulated ration and white spruce needles, respectively. Similarly, in late winter, porcupines lost 4.79 ± 1.47 $kJ \cdot kg^{-0.75} \cdot d^{-1}$ and 48.21 ± 13.78 $kJ \cdot kg^{-0.75} \cdot d^{-1}$ eating formulated ration and white spruce needles, respectively. This urinary loss was equivalent to 20 ± 3 % to 21 ± 5 % of the digestible energy intake of porcupines fed white spruce needles compared to only 1 ± 1 % to 3 ± 1 % of the digestible energy intake of porcupines fed the formulated ration.

During mid- and late winter, there was no discernable difference in maintenance N requirements for porcupines fed either diet ($f = 4.50$, $p > 0.05$); porcupines consuming either diet required 209 ± 92 $mg \cdot kg^{-0.75} \cdot d^{-1}$ to maintain nitrogen balance (Figure 2.5). Urinary N loss did not differ either between diets ($f = 1.73$, $p = 0.246$) or between mid- and late winter experimental periods ($f = 0.09$, $p = 0.781$).

Renal Response

Eighty-nine percent of urinary N excreted by porcupines fed the formulated ration was attributed to urea N ($n = 6$, $y = 1.325x + 0.010 \pm 0.021$, $r^2 = 0.897$, $p = 0.004$). Concentrations of plasma urea in all porcupines were relatively low throughout the winter, and lowest for porcupines consuming white spruce needles during mid-winter (Table 2.6). Neither osmolality of urine nor plasma changed among experimental periods for porcupines fed the formulated diet ($p > 0.775$; Table 2.6). Consequently, renal

concentration of solutes was similar among periods for individuals fed the formulated diet as indicated by urine to plasma (U/P) ratios for osmolality of 2.8 ± 1.5 in early winter, 4.2 ± 1.0 in mid-winter, and 3.6 ± 1.0 in late winter ($f = 0.47$, $p = 0.718$). In addition, diet did not affect plasma or urine osmolalities during mid-winter ($p > 0.093$; Table 2.6); U/P ratios were 3.2 ± 0.7 for white spruce and 4.6 ± 0.8 for the pelleted diet ($t = -2.123$, $df = 3.8$, $p = 0.104$). Urinary pH was similar for all winter periods (6.7 ± 0.7 in early winter, 6.7 ± 0.6 in mid-winter, and 6. 5 ± 0.4 in late winter; $p > 0.05$) and between diets (6.3 ± 0.2 for white spruce and 6.8 ± 0.6 for the formulated diet; $p > 0.05$).

Low concentrations of dietary Na in white spruce needles (0.032 ± 0.006 $mg \cdot g^{-1}$) did not allow significant retention of Na from this diet (Table 2.1, 2.4); that is, porcupines were in negative Na balance when fed white spruce needles in mid- and late winter ($p < 0.040$). In comparison, metabolizable Na intakes on the formulated diet were higher but did not vary among winter periods (Figure 2.2; Table 2.4). Metabolizable Na intake was positively correlated to Na intake of both diets ($y = 0.441x - 1.883 \pm 6.764$, $r^2 = 0.588$, $p = 0.001$). Potassium concentration was 27 % higher in the natural diet than the formulated ration (Table 2.1), yet there was no difference in digestible K intakes between diets ($f = 4.74$, $p = 0.081$; Table 2.3). Urinary Na loss ($mg \cdot kg^{-0.75} \cdot d^{-1}$) was positively related to urinary K loss ($mg \cdot kg^{-0.75} \cdot d^{-1}$) for the pelleted diet ($y = 0.412x + 2.186 \pm 0.323$, $r^2 = 0.901$, $p = 0.001$); however, there was no significant relationship between low outputs of urinary Na and K for white spruce. Urinary Na loss was affected by diet ($f = 15.93$, $p = 0.002$) and by digestible K intake ($f = 6.50$, $p = 0.025$); however, there were insufficient data to determine the type of relationship between digestible K intake and urinary Na loss. Porcupines fed white spruce needles lost only 0.42 ± 0.32 mg $Na \cdot kg^{-0.75} \cdot d^{-1}$ and 1.81 ± 1.31 mg $Na \cdot kg^{-0.75} \cdot d^{-1}$ in urine in mid- and late winter, respectively. In comparison, porcupines fed the formulated ration lost 25.05 ± 13.01 $mg \cdot kg^{-0.75} \cdot d^{-1}$ and 12.43 ± 4.48 $mg \cdot kg^{-0.75} \cdot d^{-1}$ of Na in urine during the same time periods.

Discussion

Body Mass

Captive porcupines were able to maintain body mass over winter (Figure 2.1), even though other studies have shown that wild porcupines tend to lose 30-40 % body mass throughout the winter season (Berteaux et al., 2005; Oveson, 1983; Roze, 1984; Smith, 1979; Sweitzer and Berger, 1993; Tenneson and Oring, 1985). Similarly, wild porcupines in southcentral Alaska lose up to 35 % of their fall body mass over winter (October through April; Coltrane et al., 2011; **CHAPTER 3**). Seasonal changes in photoperiod and ambient temperature have been implicated in body mass fluctuations in some temperate mammals (Dark and Zucker, 1983; Li and Wang, 2005; Nagy, 1992; Nagy, 1993; Nagy and Negus, 1993; Peacock et al., 2004; Powell et al., 2002; Voltura and Wunder, 1998). Typically, shortened photoperiod and/or cold ambient temperatures cause reductions in body mass in temperate rodents (Brenner and Lyle, 1973; Dark and Zucker, 1983; Lu et al., 2007; Peacock et al., 2004; Voltura and Wunder, 1998; Zhao and Wang, 2006). We did not observe a change in body mass in relation to temperature or day length during our study, even though average temperatures and photoperiod varied from -3.45 ± 2.88 °C and 5.86 ± 0.23 $h \cdot d^{-1}$ in early winter, to -13.89 ± 4.83 °C and 3.93 $h \cdot d^{-1}$ in mid-winter, and to -29.98 ± 4.83 °C and 14.62 $h \cdot d^{-1}$ in late winter (Figure 2.1). Reduction in body mass during winter may be an important adaptation to utilize body stores when seasonal food resources are limited (McNab, 1991; McNab, 1999; Merritt et al., 2001; Millar and Hickling, 1991). However, our results indicate that porcupines can utilize higher quality food resources opportunistically to compensate for loss in body mass. This physiological ability may have contributed to the geographic success of porcupines throughout North America.

Effect of Winter

While an endogenous pattern of body mass regulation was not evident in captive porcupines fed *ad libitum*, these animals reduced DMI during winter (Figure 2.2). Winter declines in DMI have been reported for northern ungulates fed *ad libitum* (Barboza and

Parker, 2008; Crater and Barboza, 2007; Parker et al., 1993; Taillon et al., 2006). However, most temperate rodents tend to increase DMI or energy intake (Campbell and MacArthur, 1996; Nagy and Negus, 1993; Zhao and Wang, 2006) during winter to compensate for increased thermoregulatory demands. Porcupines that consumed the formulated diet throughout the winter decreased DMI from 43.62 ± 12.73 $g \cdot kg^{-0.75} \cdot d^{-1}$ in early winter to 14.58 ± 2.06 $g \cdot kg^{-0.75} \cdot d^{-1}$ in late winter without a change in digestibility of DM (Figure 2.2). In comparison, porcupines studied by Felicetti et al. (2000) consumed 21 ± 1 $g \cdot kg^{-0.75} \cdot d^{-1}$ of a higher quality diet (4.27 % vs. 1.11 % N; 23.02 vs. 17 $kJ \cdot g^{-1}$; 14 % vs. 27 % NDF) that was more digestible (83 % vs. 72 %). Declines in DMI over winter were unexpected, because the corresponding decline in ambient temperature (Figure 2.1) typically results in increased thermoregulatory costs (Wunder, 1975, 1992).

Although digestible DMI declined (Figure 2.2), porcupines were able to maintain body mass as ambient temperatures fell. These results suggest that porcupines can decrease metabolic costs as winter progresses. Energy intakes of porcupines on the formulated ration decreased from 625 ± 137 $kJ \cdot kg^{-0.75} \cdot d^{-1}$ to 256 ± 36 $kJ \cdot kg^{-0.75} \cdot d^{-1}$ of gross energy and from 562 ± 172 $kJ \cdot kg^{-0.75} \cdot d^{-1}$ to 193 ± 33 $kJ \cdot kg^{-0.75} \cdot d^{-1}$ of digestible energy between early winter and late winter. Winter-acclimated beavers (*Castor canadensis*), a similar sized herbivorous rodent, had only a slightly higher gross energy intake of 808 ± 214 $kJ \cdot kg^{-0.75} \cdot d^{-1}$ with no change in body mass (Dyck and MacArthur, 1993). In comparison, Felicetti et al. (2000) found that porcupines maintained body mass on a pelleted ration at a digestible energy intake of 430 ± 19 $kJ \cdot kg^{-0.75} \cdot d^{-1}$, a higher intake than we observed in late winter.

On average, the maintenance energy requirement estimated for porcupines (398 $kJ \cdot kg^{-0.75} \cdot d^{-1}$) was similar to energy requirements estimated for other arboreal folivores, such as koalas (*Phascolarctos cinereus*; 388 $kJ \cdot kg^{-0.75} \cdot d^{-1}$: Ullrey et al., 1981), yet slightly higher than field metabolic rates estimated for three-toed sloths (*Bradypus variegatus*; 209 $kJ \cdot kg^{-0.75} \cdot d^{-1}$: Nagy and Montgomery, 1980). However, both koalas and sloths are not exposed to low ambient temperatures as are wintering porcupines. Furthermore, daily energy requirement for porcupines was low compared to other

eutherian mammals and some rodents (Hayssen and Lacy, 1985). Low maintenance energy requirements and/or field metabolic rates can reflect low basal metabolic rates in mammals (McNab, 1978). Basal metabolic rates for arboreal folivores are typically lower than predicted for their body mass (Arends and McNab, 2001; McNab, 1978, 1986). For example, basal metabolic rates for two-toed and three-toed sloths are 54 % and 36 % of the rates predicted by their body mass (298 $kJ \cdot kg^{-0.75} \cdot d^{-1}$: Hildwein and Goffart, 1975; Kleiber, 1947). Measures of resting metabolic rates for porcupines are less consistent (DeMatteo and Harlow, 1997; Fournier and Thomas, 1999). DeMatteo and Harlow (1997) found that the resting metabolic rate for porcupines with a LCT of 10 °C was 29 % less than the predicted metabolic rate of a mammal with this body mass (Kleiber, 1947). Comparatively, Fournier and Thomas (1999) measured a LCT of -2 °C with a BMR of 31 % to 82 % higher than expected (Kleiber, 1947). The low maintenance energy requirements indicated by our study would suggest a low BMR with a potentially low LCT.

Responses to Diet

One of the most nutritionally significant differences between experimental diets was the presence of PSM. Phenol concentration was high in white spruce needles and absent in the formulated diet (Table 2.1). White spruce needles are also known to have high concentrations of terpenes, including significant amounts of bornyl acetate, camphor, myrcene, camphene, and α-pinene (Rudloff, 1975; Yatagai and Sato, 1986). High PSM in white spruce needles corresponded with decreased DMI in porcupines; porcupines fed white spruce needles exhibited a more pronounced decline in digestible DMI compared to animals fed the formulated diet (70 % vs. 43 % decline) between mid- and late winter (Table 2.3). Our results support the detoxification limitation hypothesis, which predicts that intake is dependent on the rate at which an herbivore can detoxify PSM (Freeland and Janzen, 1974). Ultimately, saturation of detoxification substrates and/or enzymes should restrict feeding (Lawler et al., 2000; Mangione et al., 2001; Marsh

et al., 2006; Wiggins et al., 2006; Wiggins et al., 2003) and likely contributes to winter depression of DMI in porcupines.

Although porcupines maintained similar digestible intakes of energy from the formulated diet and white spruce needles, less energy was retained from the white spruce needles (up to 42 % less MEI; Table 2.4). Detoxification and elimination of PSM accounts for most of the difference in energy retention of woodrats (*Neotoma spp.*) fed natural forages (Sorensen et al., 2005). Synthesis of detoxification enzymes requires energy in addition to the cost of enzymatic reactions for conjugation and excretion, hydrolysis, oxidation and reduction. Urinary energy losses of many herbivores are increased by the excretion of conjugates, such as glucuronic acid (Cork, 1986; Mangione et al., 2004; Marsh et al., 2006). While our study did not specifically explore detoxification pathways, 20 to 21 % of digestible energy intake was lost via urine when porcupines were fed white spruce needles. Most likely a large portion of this urinary energy loss can be attributed to detoxification of PSM. For example, ruffed grouse (*Bonasa umbellus*) fed quaking aspen lost 10 % of metabolizable energy in the excretion of glucoronic acid and ornithine (detoxification conjugates) alone (Jakubas et al., 1993). Similarly, the percentage of digestible energy lost in urine was 24 % higher in woodrats fed a diet with resins compared to a control diet without PSM (Mangione et al., 2004). While the cost of detoxification may be high, porcupines may be able to minimize the energy deficit through reduction of metabolic rates during winter. For example, Boyle and Dearing (2003) found that woodrats fed juniper that was high in terpenes and phenols experienced significant decreases in resting metabolic rate (RMR). Depression of metabolic rates is well documented in animals that are responding to depressed food supply (Koteja, 1996; Rea et al., 2000; Rosen and Trites, 2000; Veloso and Bozinovic, 1993). Boyle and Dearing (2003) hypothesize that terpenes in the forage may have neurological effects which depress metabolic rate, since many terpenes have been shown to affect the central nervous system (Koppel et al., 1981).

Metabolic Responses

Our data indicate that porcupines are well adapted to exist on a low N diet even during periods of increased thermoregulatory costs. Porcupines in our study were able to maintain N balance on the formulated ration, at a N content of only 1.1 % DM. True nitrogen digestibility was high for both diets (98 ± 1 % for formulated ration and 97 ± 2 % for white spruce needles). In comparison, Felicetti et al. (2000) found that porcupines could maintain N balance on non-tannin diets of apples (0.41 % N) and a pelleted ration (4.27 % N), but Fournier and Thomas (1997) indicated that porcupines required a non-tannin diet of >1.6 % N to maintain balance. Porcupines in Felicetti's study were unable to maintain N balance on diets containing tannins that had up to 3 % N content. Furthermore, N requirements for porcupines during mid- and late winter in Alaska (209 ± 92 $mg \cdot kg^{-0.75} \cdot d^{-1}$) were lower than estimated by both Felicetti et al. (2000; 346 $mg \cdot kg^{-0.75} \cdot d^{-1}$) and Fournier and Thomas (1997; 389 $mg \cdot kg^{-0.75} \cdot d^{-1}$) and much lower than the mean for other eutherian herbivores (582 ± 235 $mg \cdot kg^{-0.75} \cdot d^{-1}$; Figure 2.5; Robbins, 1993). Previous estimates of the N requirement for porcupines were determined with diets that were free of PSM. These results are contrary to what we expected, since other studies have found that ingestion of diets with high contents of PSM result in elevated N requirements (example: Jakubas et al., 1993), as more N may be required for enzyme and substrate production to detoxify PSM. Jakubas et al. (1993) found that N requirements of ruffed grouse (*Bonasa umbellus*) were increased on diets with high concentrations of coniferyl benzoate; N was lost with excretion of detoxification conjugates, thus increasing daily N requirements. In comparison, woodrats had a relatively low N requirement (334.2 $mg \cdot kg^{-0.75} \cdot d^{-1}$) when fed a diet a high in phenolic compounds (*Juniperus monosperma*; Dearing et al., 2005a).

The majority of urinary N was probably associated with excretion of conjugated PSM, because only 20 % of urinary N was attributed to urea N in porcupines fed white spruce needles. In late winter, we found that porcupines maintained zero N balance while consuming white spruce needles. Similarly, Felicetti et al. (2000) found that porcupines fed Lodgepole pine needles were unable to maintain N balance. These results suggest

that the cost of detoxifying and eliminating PSM exceeds digestible N intake because dietary N content is low, food intake is depressed, and N is lost to processing PSM.

Renal Response

We found no indication that either water balance or acid base balance was affected by consumption of white spruce needles. Osmotic concentrations of urine relative to plasma (U/P ratio) and urinary pH were similar among experimental periods and between diets. PSM in other forages can alter renal function in some rodent species. For example, desert woodrats (*Neotoma lepida*) increase water requirements 18-30 % and fecal water loss, but not urinary water loss when fed a resin diet, because urine osmolarity is increased on the resin diet (Mangione et al., 2004). Conversely, other PSM have diuretic effects (Dearing et al., 2001). Porcupines in our study were provided snow *ad libitum*. While it is possible that PSM in white spruce may increase water intake in porcupines, our data indicate that consumption of snow was sufficient to maintain water and acid base balance. However, freezing of blood and urine samples may affect estimates of osmolality as well as pH in animals during winter. Acid-base responses of porcupines to PSM therefore require confirmation from studies in which samples of blood and urine are collected without subsequent freezing under climate-controlled laboratory conditions.

Sodium requirement of porcupines was not significantly different from zero. Therefore, wintering porcupines probably require significantly less Na than most mammals (10 $mg \cdot kg^{-1} \cdot d^{-1}$; Robbins, 1993), as do other northern herbivores, such as white-tailed deer (*Odocoileus virginianus*; 3.27 $mg \cdot kg^{-1} \cdot d^{-1}$) and ruffed grouse (7.72 $mg \cdot kg^{-1} \cdot d^{-1}$; Hellgren and Pitts, 1997; Jakubas et al., 1995). Sodium deficiencies seen in porcupines fed the white spruce diet were more directly related to low Na content than to the high loads of dietary K. Plants high in K have been shown to cause Na imbalance (Weeks and Kirkpatrick, 1976), and addition of K to feed resulted in a 76 % increase in urinary Na loss in domestic sheep (Suttle and Field, 1967). However, few studies have examined Na balance in relation to excess dietary K in non-domestic herbivores

(Christian, 1989; Christian et al., 1993). Christian (1989) found that dietary K loading in meadow voles (*Microtus pennsylvanicus*) did not impact Na balance and that Na balance was more highly correlated to Na content of diet, which suggested that meadow voles have an independent physiological ability to handle excess K (Christian, 1989). The weak response of urinary Na to digestible K intake does not allow us to conclusively determine if K regulation impacts Na balance in porcupines on a white spruce diet.

Ecological Implications

Our data suggest that during winter in Alaska, nutrition may ultimately dictate survivorship and influence the size of local populations of porcupines. Unlike many northern mammals, North American porcupines evolved in South America and migrated north across the land bridge between the two continents (Vilela et al., 2009; Woods, 1973). This evolutionary pathway may have helped porcupines evolve the physiological plasticity that enables them to persist on dietary items that are not used by other mammals, as well as the ability to gain body mass when the abundance and quality of food permits, like their neotropical relatives. These characteristics distinguish porcupines from other herbivorous northern mammals and make porcupines an extraordinarily successful species in a variety of habitats.

In Alaska, available winter forage poses additional physiological challenges due to high PSM content, low energy content, and imbalanced mineral content, while low ambient temperatures increase thermoregulatory demands. Porcupines may switch between dietary items to increase intake by varying detoxification pathways for different PSM (Dearing et al., 2005b; Freeland and Janzen, 1974) and by alleviating imbalances in mineral intake. While such behavior is typical of a generalist herbivore, porcupines possess many physiological abilities similar to specialist herbivores, such as low N requirements and the ability to handle toxin laden diets. Regardless, by the end of winter, porcupines display multiple imbalances in energy, N, and several minerals, that are only alleviated by the consumption of spring forages. Survival is therefore dependent on the

amount of body stores, the severity of winter demands and the timing of the spring (Parker et al., 2009).

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Table 2.1. Dry matter composition of diets fed to porcupines from August 2006 through April 2007.

Component	Pellets	White Spruce Needles
Gross Energy ($kJ \cdot g^{-1}$)	17.50 ± 0.07^{A}	19.16 ± 0.04^{B}
N ($g \cdot 100g^{-1}$)	1.11 ± 0.02^{A}	0.89 ± 0.04^{B}
Soluble Carbohydrate ($g \cdot g^{-1}$)	0.66 ± 0.05^{A}	0.46 ± 0.01^{B}
NDF ($g \cdot g^{-1}$)	0.27 ± 0.02^{A}	$0.48 \pm < 0.01^{B}$
Hemicellulose ($g \cdot g^{-1}$)	0.15 ± 0.04	$0.12 \pm < 0.01$
ADF ($g \cdot g^{-1}$)	$0.12 \pm < 0.01^{A}$	$0.37 \pm < 0.01^{B}$
Ash ($g \cdot g^{-1}$)	0.068 ± 0.01^{A}	0.10 ± 0.01^{B}
Phenols ($mmol \cdot g^{-1}$)	$0.01 \pm < 0.01^{A}$	0.57 ± 0.01^{B}
Na ($mg \cdot g^{-1}$)	1.48 ± 0.33^{A}	0.032 ± 0.01^{B}
K ($mg \cdot g^{-1}$)	3.24 ± 0.16	2.36 ± 0.56
Ca ($mg \cdot g^{-1}$)	6.96 ± 0.41^{A}	12.76 ± 0.50^{B}
Mg ($mg \cdot g^{-1}$)	1.54 ± 0.03	1.11 ± 0.24
Mn ($mg \cdot g^{-1}$)	$0.04 \pm < 0.01$	0.16 ± 0.18

Note: Different capital letters indicate a significant difference between diets for the component ($p < 0.05$).

Table 2.2 Digestive efficiency (digestibility) and metabolizable efficiency (metabolizability) of a formulated ration fed to porcupines (n = 3) during early winter (October), mid-winter (December), and late winter (February).

	Digestibilty (%)			Metabolizability (%)		
Component	October	December	February	October	December	February
Dry Matter	73.0 ± 5.0	70.0 ± 2.0	75.0 ± 3.0	69.0 ± 6.0	68.0 ± 2.0	51.0 ± 2.0
Gross Energy	73.2 ± 5.6	70.1 ± 1.2	75.3 ± 2.5	71.0 ± 6.2	69.1 1.0	73.4 ± 3.3
Nitrogen	68.0 ± 10.2	67.4 ± 8.1	67.9 ± 4.2	18.1 ± 26.6	44.9 ± 11.4	29.2 ± 14.2
NDF	26.4 ± 12.9	27.7 ± 4.0	27.7 ± 6.7			
Hemicellulose	38.4 ± 9.1	42.0 ± 1.4	25.3 ± 6.5			
ADF	12.0 ± 17.7	7.3 ± 7.9	30.1 ± 7.0			
Soluble Carbohydrates	94.4 ± 1.7	94.8 ± 0.9	94.7 ± 1.3			
Sodium	94.1 ± 3.8	94.4 ± 5.6	99.3 ± 0.6	24.4 ± 30.5	32.4 ± 31.7	50.4 ± 24.1
Potassium	76.6 ± 7.5	79.2 ± 13.8	96.5 ± 3.7	46.5 ± 41.9	32.3 ± 23.0	27.8 ± 37.9
Calcium	66.9 ± 5.8	68.5 ± 1.2	75.9 ± 3.7	66.9 ± 8.2	67.7 ± 1.2	75.4 ± 3.8
Magnesium	36.6 ± 10.4	36.5 ± 3.1	40.0 ± 7.3	19.9 ± 16.8	21.4 ± 7.4	31.3 ± 9.7

Table 2.3. Digestive efficiency (digestibility) and metabolizable efficiency (metabolizability) of porcupines fed white spruce needles (n = 4) during mid- (December) and late winter (February).

	Digestibilty (%)		Metabolizability (%)	
Component	December	February	December	February
Dry Matter	63.0 ± 1.0^{A}	61.0 ± 3.0^{A}	72.0 ± 4.0^{A}	49.0 ± 4.0^{B}
Gross Energy	62.3 ± 1.7^{A}	60.6 ± 3.0^{A}	49.6 ± 2.3^{A}	47.7 ± 4.5^{A}
Nitrogen	55.6 ± 5.6^{A}	30.6 ± 3.4^{B}	24.5 ± 2.3^{A}	-67.0 ± 58.0^{B}
NDF	52.6 ± 5.3^{A}	48.4 ± 5.3^{A}		
Hemicellulose	67.1 ± 28.6^{A}	36.7 ± 7.4^{B}		
ADF	48.1 ± 3.5^{A}	52.2 ± 4.7^{A}		
Soluble Carbohydrates	79.4 ± 6.7^{A}	79.8 ± 1.3^{A}		
Sodium	-30.1 ± 27.1^{A}	16.1 ± 19.9^{A}	-88.2 ± 54.8^{A}	-257.9 ± 219.8^{A}
Potassium	74.3 ± 5.0^{A}	92.2 ± 3.3^{B}	46.1 ± 3.2^{A}	78.7 ± 6.4^{B}
Calcium	67.3 ± 2.1	64.2 ± 1.9	57.4 ± 2.7^{A}	47.7 ± 5.0^{B}
Magnesium	73.2 ± 2.1^{A}	75.8 ± 5.6^{A}	37.8 ± 17.7^{A}	30.5 ± 9.9^{A}

Note: Different capital letters indicate a significant difference between time periods for the component ($p < 0.05$).

Table 2.4. Daily digestible intake of energy, plant fiber, and elements by adult porcupines fed formulated ration (n = 3) and white spruce needles (n = 4) during mid- (December) and late winter (February).

	December		February		
Component	Formulated Diet	White Spruce Needles	Formulated Diet	White Spruce Needles	Statistic (P)*
Body Mass (kg)	8.94 ± 1.10	9.33 ± 2.06	8.62 ± 2.35	9.08 ± 1.83	
Dry Matter ($g \cdot kg^{-0.75} \cdot d^{-1}$)	25.16 ± 6.05	16.75 ± 0.59	10.93 ± 1.88	11.79 ± 1.76	P (0.002), DxP (0.033)
Gross Energy ($kJ \cdot kg^{-0.75} \cdot d^{-1}$)	438.99 ± 101.51	317.72 ± 10.99	193.28 ± 33.10	223.44 ± 32.71	P (0.002), DxP (0.040)
Nitrogen ($g \cdot kg^{-0.75} \cdot d^{-1}$)	0.32 ± 0	0.17 ± 0.03	0.11 ± 0.02	0.05 ± 0.01	D (0.003), P (0.000), DxP (0.050)
NDF ($g \cdot kg^{-0.75} \cdot d^{-1}$)	3.11 ± 1.08	6.76 ± 0.73	1.02 ± 0.37	4.47 ± 0.54	D (0.003), P (0.001)
Hemicellulose ($g \cdot kg^{-0.75} \cdot d^{-1}$)	0.42 ± 0.01	0.67 ± 0.29	0.25 ± 0.07	0.37 ± 0.07	P (0.002)
ADF ($g \cdot kg^{-0.75} \cdot d^{-1}$)	0.37 ± 0.45	4.71 ± 0.33	0.56 ± 0.20	3.66 ± 0.46	D (0.000)
Soluble Carbohydrates ($g \cdot kg^{-0.75} \cdot d^{-1}$)	21.09 ± 4.80	9.65 ± 0.85	9.48 ± 1.44	7.20 ± 1.30	D (0.031), P (0.003), DxP (0.017)
Sodium ($mg \cdot kg^{-0.75} \cdot d^{-1}$)	39.23 ± 10.24	-0.21 ± 0.19	26.28 ± 3.81	0.10 ± 0.11	D (0.001), P (0.035), DxP (0.030)
Potassium ($mg \cdot kg^{-0.75} \cdot d^{-1}$)	92.52 ± 26.89	54.49 ± 4.82	43.29 ± 6.03	34.91 ± 4.84	P (0.004)
Calcium ($mg \cdot kg^{-0.75} \cdot d^{-1}$)	165.17 ± 33.88	234.27 ± 7.89	74.50 ± 12.99	153.87 ± 25.62	D (0.023), P (0.001)
Magnesium ($mg \cdot kg^{-0.75} \cdot d^{-1}$)	20.62 ± 6.28	18.21 ± 1.00	8.89 ± 2.67	18.87 ± 4.28	P (0.033), DxP (0.028)

* Significance ($P < 0.05$) of the effects of Diet (D) , Period (P) and interaction between Diet and Period (D x P).

Table 2.5. Daily metabolizable intake of dry matter, energy, and elements by adult porcupines fed formulated ration (n = 3) and white spruce needles (n = 4) during mid- (December) and late winter (February).

	December		February		
Component	Formulated Diet	White Spruce Needles	Formulated Diet	White Spruce Needles	Statistic (P)*
Body Mass (kg)	8.94 ± 1.10	9.33 ± 2.06	8.62 ± 2.35	9.08 ± 1.83	
Dry Matter ($g \cdot kg^{-0.75} \cdot d^{-1}$)	24.64 ± 6.00	13.60 ± 0.20	10.54 ± 1.97	9.42 ± 1.37	P (0.002) DxP (0.025)
Gross Energy ($kJ \cdot kg^{-0.75} \cdot d^{-1}$)	432.64 ± 100.51	252.64 ± 4.72	188.49 ± 34.38	175.23 ± 24.49	D (0.002) DxP (0.025)
Nitrogen ($g \cdot kg^{-0.75} \cdot d^{-1}$)	0.21 ± 0.05	0.07 ± 0.01	0.05 ± 0.03	-0.11 ± 0.12	D (0.009) P (0.005)
Sodium ($mg \cdot kg^{-0.75} \cdot d^{-1}$)	14.18 ± 15.74	-0.63** ± 0.39	13.85 ± 7.60	-1.71** ± 1.31	D (0.050)
Potassium ($mg \cdot kg^{-0.75} \cdot d^{-1}$)	40.48 ± 36.84	33.79 ± 2.36	14.07 ± 17.39	29.71 ± 3.86	
Calcium ($mg \cdot kg^{-0.75} \cdot d^{-1}$)	163.23 ± 34.09	199.60 ± 7.08	74.02 ± 13.06	114.14 ± 20.49	P (0.001)
Magnesium ($mg \cdot kg^{-0.75} \cdot d^{-1}$)	12.46 ± 6.98	9.31 ± 4.00	7.02 ± 2.86	7.54 ± 2.52	

* Significance ($P < 0.05$) of the effects of Diet (D), Period (P) and interaction between Diet and Period (D x P).

** Means are significantly different from 0 ($p < 0.04$)

Table 2.6. Composition plasma and urine of porcupines fed a formulated diet (n = 7) and white spruce needles (n = 8) in early (October), mid- (December) and late winter (February).

	Early Winter	Mid-Winter		Late Winter	
	Formulated Ration	Formulated Ration	White Spruce Needles	Formulated Ration	White Spruce Needles
Urea N in Plasma ($mg \cdot ml^{-1}$)	0.13 ± 0.02	0.14 ± 0.03	0.04 ± 0.03	0.12 ± 0.02	NA
Urea N In Urine ($mg \cdot ml^{-1}$)	0.15 ± 0.05	0.24 ± 0.07	0.07 ± 0.03	0.26 ± 0.02	0.08 ± 0.05
Osmolarity of Plasma	279.5 ± 3.8	274.8 ± 8.6	281.6 ± 3.2	269.0 ± 7.5	NA
Osmolarity of Urine	785.6 ± 407.3	1162.8 ± 288.2	927.1 ± 154.1	1225.1 ± 19.6	788.3 ± 127.2

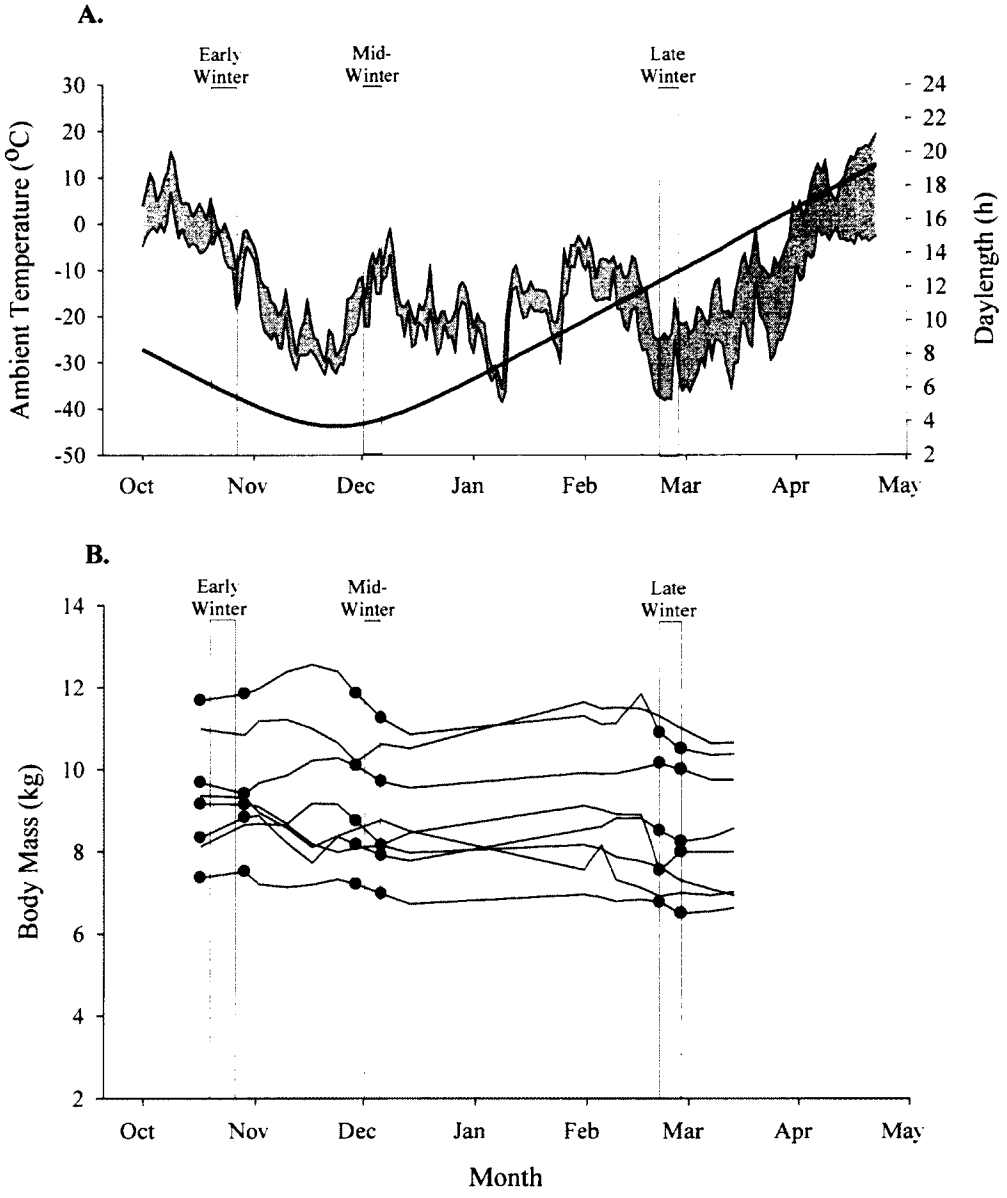

Figure 2.1. A. Duration of daylight (solid line, h·d-1) and air temperature (shaded area between daily maximum and minimum, °C) in Fairbanks, Alaska from October 2006 through April 2007. Open bars indicate the periods of sample collections in early winter (October 20-26, 2006), mid-winter (December 1-5, 2006), and late winter (February 22-26, 2007). B. Body mass (kg) of captive porcupines (n = 8) recorded from October 2006 through April 2007. Closed circles indicate animals (n = 5) fed white spruce needles during experimental periods in early, mid- and late winter. All animals were fed pellets between experimental periods.

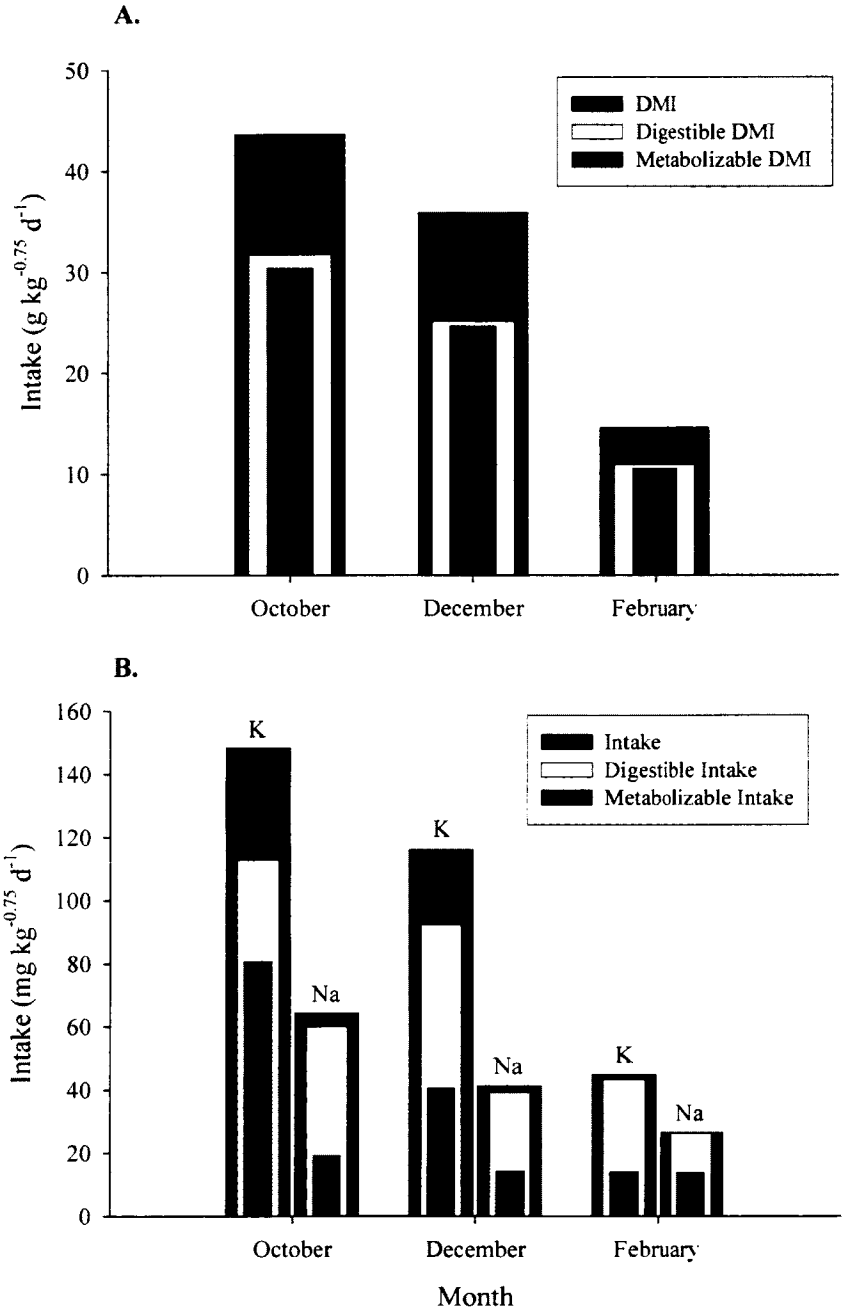

Figure 2.2. Intakes of captive porcupines fed a formulated ration (n = 3) during early (October), mid- (December), and late winter (February) of 2006-2007 in Fairbanks, Alaska. A. Total, digestible, and metabolizable intakes of dry matter. B. Total, digestible, and metabolizable intakes of K and Na (B.).

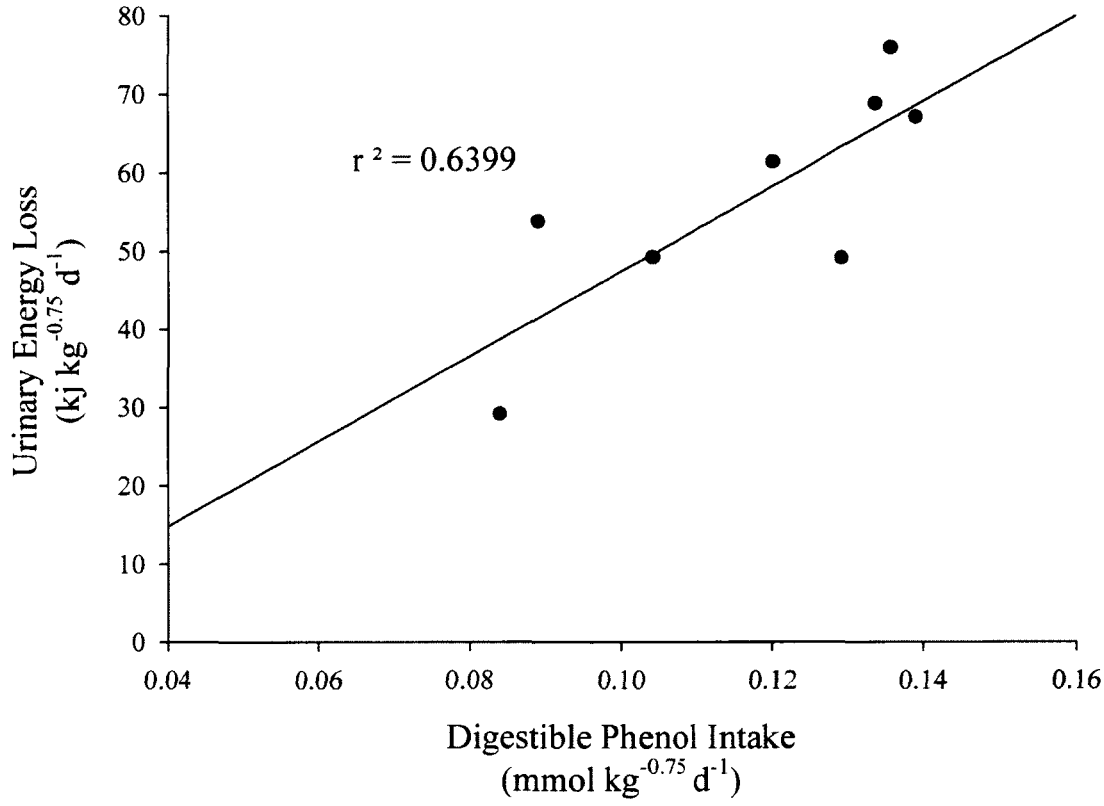

Figure 2.3. Regression of urinary energy loss ($kJ \cdot kg^{-0.75} \cdot d^{-1}$) against digestible phenol intake ($mmol \cdot kg^{-0.75} \cdot d^{-1}$; $y = 537.943x - 6.294 \pm 9.647$, $r^2 = 0.635$, $p = 0.018$) for porcupines fed white spruce needles ($n = 8$) during winter 2006-2007 in Fairbanks, Alaska.

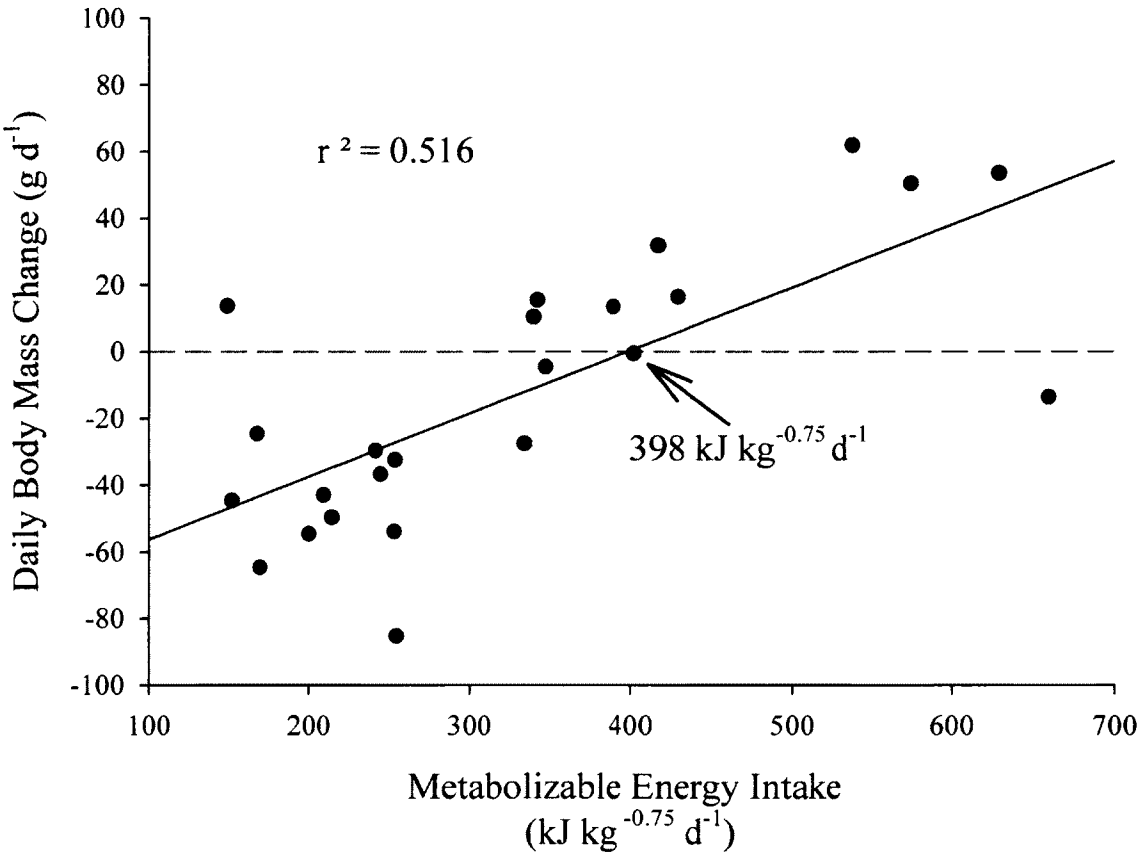

Figure 2.4. Regression of daily metabolizable energy intake (kJ·kg-0.75·d-1) against daily mass change ($g \cdot d^{-1}$; $y = 0.189x - 75.144 \pm 28.132$, $r^2 = 0.516$, $p < 0.001$) for porcupines ($n = 24$) during winter in Fairbanks, Alaska. Minimum daily energy requirement was calculated as energy consumption at zero daily mass change (398 ± 28 $kJ \cdot kg^{-0.75} \cdot d^{-1}$).

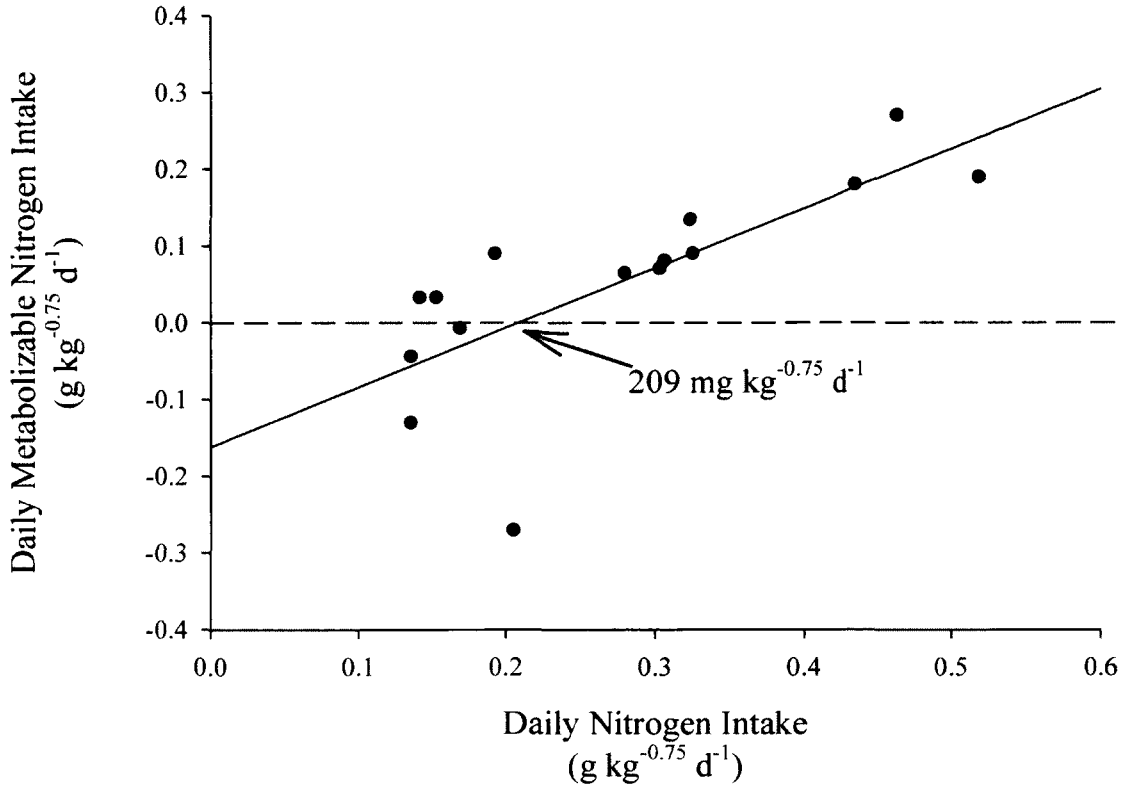

Figure 2.5. Regression of metabolizable nitrogen intake against nitrogen intake ($g \cdot kg^{-0.75} \cdot d^{-1}$) in captive porcupines fed a formulated ration (n = 7) and white spruce needles (n = 8) during mid- and late winter in Fairbanks, Alaska. Minimum daily nitrogen requirement was 209 ± 92 $mg \cdot kg^{-0.75} \cdot d^{-1}$ ($y = 0.776x - 0.162 \pm 0.092$, $r^2 = 0.547$, $p = 0.002$).

CHAPTER 3 - SEASONAL BODY COMPOSITION, WATER TURNOVER, AND FIELD METABOLIC RATES IN PORCUPINES (*ERETHIZON DORSATUM*) IN ALASKA[a]

Abstract

Winter extremes of temperature and food shortage limit the distribution of arctic animals. North American porcupines (*Erethizon dorsatum*) are one of the most widely distributed mammals in North America and range from deserts to arctic tundra. In Alaska porcupines remain active at low winter temperatures (i.e., -39 °C) while consuming woody plants that are low in nitrogen (N) and high in both fiber and plant secondary metabolites. Porcupines conserved lean body mass in winter by using fat stores. Fat mass declined from 50 ± 3 % to 27 ± 7 % of body mass over winter. Animals with small fat stores might be more reliant on food intake during winter, because proportional fat loss was correlated positively with total fat mass at the start of winter. Fat losses were minimized by lowering rates of energy expenditure. Field metabolic rate was 440 ± 18 kJ · $kg^{-0.77}$ · d^{-1}. Water turnovers were slow at 26.62 ml · $kg^{-0.75}$ · d^{-1} in wild porcupines. Body temperatures were not reduced to save energy; core temperatures were maintained at 37.3 ± 0.1 °C despite variation in ambient air temperature from +7 to -38 °C in captivity. Persistence of porcupines at the northern limits of their range is due to plasticity of food intake, tolerance of low-quality diets, and low ambient temperatures. Minimal expenditures of energy and N in winter are combined with the conservation of lean mass. Porcupines rely on abundant summer forages to replenish their stores of fat and protein for reproduction and survival in the subsequent winter.

Introduction

Winter is a period of decreased food availability and quality that limits the population size of many northern herbivores (Blix 2005; Marchand 1996; White et al. 1987). Seasonal shifts in body composition and mass, and reduction in energy

[a]Coltrane, J. A., S. Farley, P. S. Barboza, F. Kohl, R. Sinnott, and B. M. Barnes. 2011. Seasonal body composition, water turnover, and field metabolic rates in North American porcupines (*Erethizon dorsatum*) in Alaska. Journal of Mammalogy 92(3): 601-610.

expenditure enable some herbivores to survive the hardships of winter (Adamczewski et al. 1997; Blix 2005; Holand 1992; Marchand 1996; Reimers et al. 1982; Virgl and Messier 1992; White et al. 1987). Most northern herbivores accumulate fat stores during late summer and fall and then catabolize those stores when food intake falls below energy requirements in winter (Holand 1992; Husband 1976; Reimers et al. 1982). However, some small herbivores, such as rodents, can alter the mass and activity of their lean tissues to reduce basal energy requirements during winter (Brenner and Lyle 1974; Dark and Zucker 1983; Lu et al. 2007; Peacock et al. 2004; Voltura and Wunder 1998; Zhao and Wang 2006). Rodents can reduce total energy expenditure further by decreasing foraging activity through the use of food caches, increasing insulation, using microclimates to reduce overall heat loss, as well as by decreasing body temperature and metabolic rate during torpor and hibernation (Fietz et al. 2005; Landry-Cuerrier et al. 2008; Long et al. 2005).

North American porcupines (*Erethizon dorsatum*) are medium-sized (< 15 kg) herbivores (Woods 1973) that remain active in winter while consuming woody plants that are low in nitrogen (N) and high in both fiber and plant secondary metabolites (PSM), such as tannins, terpenes, and other phenolic compounds (Griesemer et al. 1998; Roze 1984, 1989; Sweitzer 1996; Tenneson and Oring 1985). Captive porcupines fed a natural diet of white spruce needles (*Picea glauca*) apparently digested 87-92 % of dietary phenols and lost 21% of their digestible energy intake via urine, which reduced retention of energy by 42 % when compared with porcupines maintained on a formulated diet free of phenolic PSMs (Coltrane and Barboza 2010; **CHAPTER 2**). Consequently, porcupines typically lose body mass and have a high risk of winter mortality due to starvation (Berteaux et al. 2005; Oveson 1983; Roze 1984; Smith 1979; Sweitzer and Berger 1993; Tenneson and Oring 1985). In Alaska winter is a nutritional bottleneck for porcupines, because low-quality food must be used when low ambient temperatures simultaneously increase thermoregulatory demands (Coltrane and Barboza 2010; **CHAPTER 2**). Although porcupines have adapted to nutritional challenges in winter, they must rebuild body stores

of energy, protein, and other nutrients by consuming forages that become available in the spring (Coltrane and Barboza 2010; **CHAPTER 2**).

Porcupines might be able to cope with winter deficits of energy and nutrients by changing body composition and mass to reduce metabolic costs. Previous studies have implied that an overwinter decrease in body mass is indicative of poor body condition and poor forage quality (Roze 1984; Sweitzer and Berger 1993). However, absolute daily energy expenditure is lowered by reducing metabolic body mass (McNab 1971). Furthermore, inadequate energy and protein intake can be offset by catabolizing lipid reserves and lean tissue throughout winter. Reducing daily activity and entering daily torpor also could decrease energy requirements and enhance winter survival.

Captive porcupines conserved body mass throughout an Alaskan winter when provided with a diet free of PSM. These captive animals expended little energy (Metabolic Energy Intake: 398 $kJ \cdot kg^{-0.75} \cdot d^{-1}$) to maintain body mass, even when ambient temperatures decreased to -39 °C (Coltrane and Barboza 2010; **CHAPTER 2**). We examined the ability of porcupines to conserve lean body mass through seven months of winter in Alaska by measuring body composition of captive and free-ranging wild porcupines. Further, we estimated energy expenditures from net changes in body tissue and the requirement for maintenance of body mass. In addition, we calculated rates of water turnover as an index of energy expenditure. Core body temperatures were monitored throughout winter to test the hypothesis that porcupines used labile body temperatures to reduce energy expenditures. In comparison with captive porcupines, we predicted that free-ranging porcupines would incur additional costs for activity and lose more body fat and lean mass due to the metabolism of PSM in their winter diet.

Materials and Methods

Subjects

We captured 38 porcupines between August 2005 and January 2008 using dip nets or live traps in Anchorage (n = 36; N 61° 10.2', W 150° 1.2') and Fairbanks (n = 2; N 64° 49.2', W 147° 52.2'), Alaska. All individuals were classed as adults (> 2 years) or

juveniles (< 2 years) based on tooth eruption patterns and body mass (adults: > 5 kg; Dodge 1982). All procedures and handling protocols were approved by the Institutional Animal Care and Use Committee, University of Alaska Fairbanks (UAF; protocol 06-027) and were consistent with guidelines approved by the American Society of Mammalogists (Gannon and Sikes 2007).

Ten adult porcupines captured in the summer of 2006 were transported to the Biological Reserve at the University of Alaska Fairbanks for the captive portion of this study (August 2006 through April 2007). Porcupines were housed in individual pens (1.22 m x 1.83 m x 2.44 m) equipped with climbing structures and a plastic den (0.46 m x 0.46 m x 0.61 m) filled with straw. The plastic den provided a microenvironment to help reduce thermoregulatory demands and simulate natural dens used by porcupines in the wild. Pens were located outdoors in a roofed wire and plywood enclosure, which was exposed to ambient temperatures, but protected from precipitation and some wind. Porcupines were provided with food and water or snow *ad libitum*. Animals were fed a pelleted ration (Alaska Mill and Feed, Anchorage, Alaska) formulated to mimic the low concentration of N in a natural diet while still maintaining adequate concentrations of minerals and trace nutrients (Barboza and Parker 2008). We recorded body mass (± 0.01 kg, AE Adams CPW Plus 35; Adam Equipment Inc., Danbury, CT) each week. Ambient air temperatures at the captive facility were recorded every 0.5 h (HOBO Pro Series Temp; ONSET, Pocasset, Massachusetts) throughout the study.

Hobo StoAway TidBit TBICU32-05+44 temperature loggers (ONSET), purchased unpotted and covered with shrink-wrap and waterproof wax before gas sterilization (Long et al. 2007), were implanted in the abdominal cavities of captive porcupines (n = 7) to record body temperatures (± 0.01 °C) every 20 min. Loggers weighed 12 – 14 g. All surgical procedures were approved by the Institutional Animal Care and Use Committee, UAF (surgical supplement #06-06).

The remaining porcupines (n = 28) were immobilized with Telazol ($5g \cdot kg^{-1}$; Fort Dodge Animal Health, Fort Dodge, Iowa) and then fitted with very high-frequency (VHF) radio collars (model 225; Telonics, Inc., Mesa, Arizona), and released at the

capture site or within Far North Bicentennial Park (N 61° 9', W 149° 45' W) in Anchorage. Average daily ambient air temperatures were recorded daily at the Campbell Creek Science Center, Anchorage (N 61° 09.843', W 149° 46.625'), which was located within the study site.

Body Composition Analysis

We determined the total amount of water in the body pool for captive and free-ranging porcupines during fall (October through November), mid-winter (late December through early February), and spring (April through May) using the deuterium oxide dilution method (Lifson and McClintock 1966). Porcupines were weighed (± 0.01 kg) and then immobilized using Telazol as described above. Once porcupines could be handled safely, we administered an oral dose of deuterated water (D_2O 99.9 %; Aldrich Chemicals, Saint Louis, Missouri) at approximately 1 mg · kg^{-1} body mass, followed by an oral flush of 9 cc of distilled water. We collected blood samples before administration of D_2O and after equilibration at 3 h from the dose. The 3-h equilibration period was established from a preliminary study, during which blood samples were drawn and analyzed every 15 to 30 min to determine the amount of time necessary to reach equilibrium. Blood was drawn from the jugular vein with a 23-gauge x 0.25-cm needle and transferred to either a 4.0-ml vacutainer tube that contained lithium heparin or a 5.0-ml vacutainer tube that contained a clot activator (Becton Dickinson, Franklin Lakes, New Jersey). Plasma was separated from red blood cells by centrifugation (3,000 x *g* for 10 min) for samples collected in lithium heparin. Water was vacuum sublimated from whole blood samples. All samples were frozen at -20 °C until analysis. Urine was collected opportunistically after isotope equilibration and stored in cryotubes (Nunc, Roskilde, Denmark).

Samples (approximately 40 µl of sublimated water or plasma) were diluted with 3 ml distilled water into 3.6-ml cryotubes (Nunc), and D_2O concentration was measured with a continuous flow IRMS (20-20 Stable Isotope Analyser; Europa Scientific Ltd, Crewe, United Kingdom) interfaced with an elemental analyser unit (ANCA-NT system,

solid/liquid preparation module; Europa Scientific) using methodology described by Scrimgeour et. al (1993). Water content of plasma was determined by drying to a constant mass at 70 °C. Plasma D_2O concentrations were expressed on the basis of water content (92 ± 1 % of plasma mass). The D_2O space was calculated by dividing the dose by the net concentration of D_2O in plasma water at equilibration (g D_2O · g plasma water^{-1}). Total body water was calculated as D_2O space divided by 1.09 to correct for overestimation of body water by D_2O dilution (Barboza et al. 2004). Ingesta free mass and tissue water space were calculated by determining digesta mass and digesta water content, respectively, from freshly killed porcupines (n = 13) collected in April before green-up and in August. Animals not dissected immediately were wrapped thoroughly in plastic to minimize desiccation during storage at -20 °C. Digesta was removed from the tract, and water content was determined by drying to a constant mass at 60 °C. Whole body mass contained 18 ± 5 % digesta, which was 84 ± 2 % water. Ingesta free mass was calculated by subtracting average digesta mass (18 %) from whole body mass. Tissue water space calculated by total body water dilution was corrected by subtracting 14.9 % of body mass, which was the average amount of water in the digestive tract. Fat-free mass was assumed to contain 72 % water (Speakman 2001). Body fat content was calculated as the difference between ingesta free mass and lean mass.

Water Turnover Rate

Water turnover rates were estimated (±1 ml · kg$^{-0.75}$ · d^{-1}) in mid-winter (January) for free-ranging porcupines (n = 13), and during fall (October) and mid-winter (January) for captive porcupines (n = 10 and n = 9, respectively). We used samples of plasma or urine to calculate turnover rates and turnover times of the body water pool by estimating the rate of disappearance of D_2O (Barboza et al. 2004). Plasma and urine can be used interchangeably and provide identical D_2O values (Speakman 2001). Urine samples were collected from captive animals for up to 4 days following initial dosing. Free-ranging animals were captured up to 13 days after D_2O dosing (6 ± 3 days) to obtain blood samples as described above. Samples were subsequently thawed and analyzed for D_2O

concentration, which was expressed on the basis of water content in each sample. Water turnovers were expressed on the basis of metabolic body mass with the scalar 0.75 (Nagy et al. 1999).

Field Metabolic Rate

Mid-winter field metabolic rates (FMR) were estimated for free-ranging porcupines (4 females and 4 males). FMR was calculated by adding the maintenance energy requirement (metabolizable energy intake at 0 mass change: 398 kJ · $kg^{-0.75}$ · d^{-1}— Coltrane and Barboza 2010) to the energy expenditure calculated from any daily changes in fat and lean mass over the winter (Barboza et al. 2009). Maintenance energy requirements were determined by mass balance in captive porcupines fed known quantities and composition of food (Coltrane and Barboza 2010). The energy content of fat was assumed to be 39.3 kJ · g^{-1} (Barboza et al. 2009; Blaxter 1989). Lean tissue was assumed to be 23 % protein (Husband 1976) with an energy content of 23.7 kJ · g^{-1} (Barboza et al. 2009; Blaxter 1989). We assumed that energy from catabolism of fat and lean tissue was converted to metabolizable energy at 82 % efficiency, as determined in several mammals (Barboza et al. 2009; Blaxter 1989). We used 0.77 as the scalar of body mass for FMR based on the interspecific relationship of Nagy et al. (1999) for eutherian mammals.

Statistical Analysis

Statistics were analyzed with modules in SYSTAT 11 (SYSTAT Software, Richmond, California). We tested parametric assumptions of normality using Shapiro-Wilk test, and we used Lavene's test to determine if variances were homogenous. Repeated measures of body mass and composition of captive porcupines were compared among seasons by 1-way ANOVA. Difference in body masses between males and females were determined using a 2-sample *t*-test. Body mass of free-ranging porcupines were compared among years using 1-way ANOVA. Body mass and composition (fat and lean tissue mass) of free-ranging porcupines were compared among seasons using ANCOVA (*F*), with individual and date as covariates. Pairwise contrasts were performed

with Bonferroni adjustments for multiple comparisons among periods. Field metabolic rates were compared between sexes using a 2-sample *t*-test. Data expressed as proportions or percentages were transformed to the arcsine of the square root to meet assumptions of normal distribution (Zar 1999). Statistical significance was determined as $\alpha < 0.05$. Means (± *SD*) are reported. Linear regressions (R^2) are reported with the *SE* of the estimate.

Results

Winter Conditions

Minimum daily ambient air temperatures within the captive enclosure in Fairbanks, Alaska, ranged from 7 °C on 9 October 2006 to -38 °C on 9 January 2007 for the winter period (1 October through 23 April; Fig. 3.1A), with a total of 153 days below -10 °C (estimated Lower Critical Temperature, LCT, for porcupines—DeMatteo and Harlow 1997). Day length ranged from 3.72 h · d^{-1} on 19 to 23 December 2006 to 16.10 h · d^{-1} on 23 April 2007 (Fig. 3.1A). At the field study site in Anchorage ambient winter air temperatures ranged from -31 °C to 12 °C in 2005/2006, -33 °C to 18 °C in 2006/2007, and -32 °C to 17 °C in 2007/2008. Total time spent below LCT was 119, 142, and 116 days in the three consecutive winters (1 October through 15 May; Fig. 3.2A). Average annual day length ranged from 17.50 ± 0.03 h · d^{-1} on 15 May to 5.45 ± 0.00 h · d^{-1} on 20-22 December (Fig. 3.2A).

Body Mass and Composition of Captive Porcupines

Body mass of captive porcupines did not change significantly across the sampling periods between October through April (Fig. 3.1B; $F_{3,24} = 0.790$, $P = 0.509$). In the fall males were not larger than females ($t_7 = -1.134$, $P = 0.294$), and the proportion of fat and lean mass was similar between sexes during all collection periods (mid-October: $t_{6.9} = -0.398$, $P = 0.703$ and $t_{2.7} = -0.769$, $P = 0.504$; late October: $t_{3.3} = -0.381$, $P = 0.726$ and $t_7 = -2.344$, $P = 0.060$; December: $t_{3.9} = -0.742$, $P = 0.500$ and $t_7 = -1.366$, $P = 0.214$; April: $t_{5.3} = -1.168$, $P = 0.292$ and $t_{3.6} = -1.659$, $P = 0.180$, respectively, for fat and lean mass).

Therefore both sexes were pooled for further body composition analysis. Fat mass ($F_{3,21}$ = 6.594, P = 0.007) and lean mass ($F_{3,21}$ = 15.582, P = 0.006) were directly related to body mass, and therefore the amount of fat and lean tissue did not vary over winter when body mass was used as a covariate (fat: $F_{3,21}$ = 1.007, P = 0.409; lean: $F_{3,21}$ = 1.125, P = 0.362; Fig. 3.1B).

Body Mass and Composition of Free-ranging Porcupines

Winter body mass of male and female free-ranging porcupines did not vary among years (females: $F_{2,8}$ = 33.319, P = 0.253; males: $F_{2,6}$ = 25.860, P = 0.126). Fall body mass of males (n = 8) was greater than that of females (n = 11; 10.62 ± 1.92 kg versus 7.80 ± 1.68 kg; T_{17} = 2.109, P = 0.003), but males and females lost mass at similar rates through winter (18 ± 6 g · d^{-1} and 13 ± 4 g · d^{-1}, respectively; $F_{1,16}$ = 1.241, P = 0.294) and among years ($F_{2,16}$ = 1.899, P = 0.219; Fig. 3.2B; Table 3.1). By spring porcupines had lost 34 % of their fall body mass, at an average rate of 17 ± 6 g · d^{-1} over the winter (Fig. 3.2B). Individual accounted for most of the variation in mass loss described by a general linear model with Julian day, individual, sex, and season as independent variables (R^2 = 0.89, $F_{2,45}$ = 1.783, P < 0.001).

Although fat mass for both sexes decreased at an average rate of 13 ± 5 g · d^{-1}, lean mass did not change significantly over winter (Table 3.1). In fall, fat mass was 50 ± 3 % of total body mass (n = 9) but only 27 ± 7 % (n = 8) of spring body mass for those individuals that survived the duration of the winter. Winter fat loss was related positively to fall fat mass ($F_{1,8}$ = 17.902, P = 0.003; Fig. 3.3) but not significantly related to lean mass ($F_{1,8}$ = 1.973, P = 0.198).

Body Temperature, Water Flux, and Field Metabolic Rate

Between 1 October 2006 and 3 April 2007 the daily average of core body temperature was 37.34 ± 0.09 °C (n = 7); daily average maxima and minima were 37.95 ± 0.09 °C and 36.87 ± 0.29 °C, respectively (Fig. 3.4). No use of daily torpor, defined as Tb < 34 °C, was recorded in captive porcupines, and instead Tb was maintained almost exclusively within a range of 36.5 to 38.0 °C. Water turnover rates for captive porcupines

were estimated for fall (October, $n = 10$) and mid-winter (December, $n = 9$). However, due to the short duration of the collection period, the rate of decline in D_2O concentration was significant only for 4 porcupines in the fall and for 3 porcupines in mid-winter. For these 7 individuals the total turnover time of the body water pool was 19 ± 5 days, which was similar to the total turnover time of free-ranging porcupines in mid-winter (Table 3.2). Water turnover rates did not differ between captive and free-ranging porcupines (Table 3.2). However, based on lean mass, water turnover rates were higher in captive compared to free-ranging porcupines. Captive porcupines lost 43 ± 17 $g \cdot kg^{-1} \cdot d^{-1}$ via feces compared to 10 ± 3 $g \cdot kg^{-1} \cdot d^{-1}$ via urine.

We found no difference in estimated FMR for free-ranging males ($n = 4$) and females ($n = 4$) during mid-winter ($T_{7.3} = -0.904$, $P = 0.395$; Table 3.3). For both sexes combined FMR was 440 ± 18 $kJ \cdot kg^{-0.77} \cdot d^{-1}$ on the basis of whole body mass and 1,232 ± 147 $kJ \cdot kg^{-0.77} \cdot d^{-1}$ on the basis of lean body mass.

Discussion

Free-ranging porcupines exhibit a seasonal variation of body mass and composition that is not apparent in captive porcupines maintained under similar environmental conditions, including similar ambient temperatures and den structures (Coltrane and Barboza 2010; **CHAPTER 2**). Food quality may be a principal constraint on maintenance of mass in free-ranging porcupines. Winter mass loss does not appear to be endogenously controlled, because captive porcupines maintain body mass on a diet free of PSM (Coltrane and Barboza 2010; **CHAPTER 2**). Similar proportional losses in body mass over winter (34 % of fall mass) and subsequent summer mass gain have been reported for porcupines from various habitats and latitudes in North America (Berteaux et al. 2005; Roze 1984; Smith 1979; Sweitzer and Berger 1993; Tenneson and Oring 1985). This plasticity in the regulation of body mass enables porcupines to exploit higher quality food sources whenever they are available. A flexible response to food would allow porcupines to restore and regain body mass in a wide range of variable habitats.

The seasonal variation in body mass in free-ranging porcupines is associated primarily with changes in fat mass, as lean mass remains relatively constant year round. Although we did not determine body composition on a monthly basis, our data indicate that the majority of fat gain occurs in late summer through fall (July – October). Peak fat mass is obtained at the onset of a seasonal decline in food quality. Use of fat stores coincides with a dietary shift to winter forages that are low in digestible energy and high in PSM. Porcupines probably reach their lowest fat mass in late spring (late May) because fat was still 27 % of body mass at the time of the spring collection period (March - April), which preceded the emergence of spring vegetation. Sampling occurred at least three weeks before new foliage began to appear and at least a month before a significant diet switch occurred. Therefore, fat reserves probably were necessary to meet daily energy requirements for at least another month beyond when porcupines were sampled. Similar patterns of fat accumulation and catabolism are displayed in larger-bodied northern herbivores (primarily ungulates) that remain active during winter (Adamczewski et al. 1997; Barboza et al. 2004; Holand 1992; Parker et al. 1993). For example, European roe deer (*Capreolus capreolus*) deposit fat until late fall and deplete fat stores from early January to April (Holand 1992). Similarly, black-tailed deer (*Odocoileus hemionus sitkensis*) catabolize 70-82 % of their body fat from October through March, which accounts for 82-92 % of total catabolized energy over the winter (Parker et al. 1993). Assuming the energy content of fat is 39.3 kJ $\cdot$ g^{-1}, catabolism of fat stores (at 82 % efficiency) during winter provided porcupines with 411 $\pm$ 160 kJ $\cdot$ d^{-1} or 72 $\pm$ 22 kJ $\cdot$ $kg^{-0.75}$ $\cdot$ d^{-1}, which was equivalent to 13-24% of their estimated daily maintenance energy requirement (398 kJ $\cdot$ $kg^{-0.75}$ $\cdot$ d^{-1}—Coltrane and Barboza 2010; **CHAPTER 2**). Hence, porcupines forage to meet 75 – 90% of their daily energy requirement in winter.

Compared to other northern non-hibernating rodent species, the porcupine has a unique ability to accumulate and use large fat stores during winter. Most rodents depend on food caches and other physiological strategies to survive winter food shortages. For example, muskrats (*Ondatra zibethicus*) rely heavily on cached food supplies; fat is deposited until late February, and catabolism of fat stores occurs only in late winter when

cached food approaches depletion (Virgl and Messier 1992). Fat levels in non-hibernating, small-bodied rodents are typically only 3-8 % of body mass (Batzli and Esseks 1992). A presumption is that the accumulation of fat often results in reduced mobility, thus subjecting animals to increased rates of predation (Batzli and Esseks 1992). Porcupines may reduce their exposure to predation by being heavily defended with quills and by dramatically reducing their daily activity and movements (Roze 1989). We observed individuals that remained in a single tree or multi-tree complex for up to a month without descending.

Unlike most northern herbivores, porcupines maintain lean mass over the winter (Adamczewski et al. 1997; Barboza and Parker 2008; Dark and Zucker 1983; Holand 1992; Parker et al. 1993; Voltura 1997; this study). This result was unexpected, as winter diet is low in N and energy (Coltrane and Barboza 2010; **CHAPTER 2**) when thermoregulatory costs are high. Porcupines are well adapted to exist on low N diets (Felicetti et al. 2000), even when the diets are high in PSM (Coltrane and Barboza 2010; **CHAPTER 2**). Nitrogen requirements for porcupines during mid and late winter in Alaska (209 ± 92 mg·kg$^{-0.75}$d^{-1}; —Coltrane and Barboza 2010; **CHAPTER 2**) are much lower than the mean for other eutherian herbivores (582 ± 235 mg·kg$^{-0.75}$d^{-1} —Robbins 1993). Porcupines appear to minimize whole body protein synthesis during winter as a response to diet. For example, quills lost by free-ranging porcupines are not replaced during winter. In comparison, captive porcupines maintained on a formulated diet without PSM grow quills during winter and suffer less quill loss in general (J.A. Coltrane, pers. obs.).

Porcupines probably maintain lean mass by combining low N requirements with an ability to spare body protein while using large fat stores (Barboza et al. 2009). Fasting polar bears display a high degree of variation of protein catabolism among individuals (Atkinson et al. 1996); bears with larger fat stores at the onset of fasting catabolize little to no body protein while fasting (Atkinson et al. 1996). Similarly, it is possible that porcupines with insufficient fat reserves to survive winter might be forced to catabolize body protein as the season progresses.

The rate of winter mass loss for individual porcupines was not affected by their lean mass but depended on the amount of fat they possessed in the fall. Although adult free-ranging male porcupines were larger than adult free-ranging females in the fall, we found no difference between the sexes in the proportion of body mass that was fat. Therefore, due to sexual dimorphism in porcupines, males lose larger absolute amounts of fat mass than females, but the proportion of body mass lost as fat is similar between the sexes. Sexual variation in the deposition and use of fat stores has been linked to the reproductive cycle of several species of mammals (Adamczewski et al. 1997; Barboza and Bowyer 2001; Barboza et al. 2004; Holand 1992; Voltura 1997; Winstanley et al. 1999). For example, peak body fat (13 % of body mass) in male red foxes (*Vulpes vulpes*) occurs in June right before breeding, whereas females attain peak body fat (16 % body mass) in July during gestation (Holand 1992). The similarity in body mass and fat cycles between male and female porcupines is most likely a reflection of timing and costs of reproductive effort. Breeding occurs in the fall and early winter (Roze 1989), followed by relatively long gestation of 210 days (Shadle 1948, 1951). Young porcupines are precocial and can survive on vegetation within one to two weeks after birth (Dodge 1982). Therefore, female porcupines can distribute energy costs of reproduction over a long gestation and a short lactation period. A similar tactic is used by the cavy (*Cavia magna*), a hystricomorph rodent with unusual reproductive patterns similar to those of the porcupine. A long gestation in the cavy does not result in an increase in daily FMR (Kunkele et al. 2005). One might expect a long gestation to have a similar impact on the daily metabolic demands of porcupines. Although this strategy is typical for slowly reproducing, long-lived ungulates, it is uncommon for most rodents (Promislow and Harvey 1990). In addition, the cost of lactation in porcupines is low. Lactation increases daily energy intake only by 17 % (Farrell and Christian 1987), whereas intake increases by up to 150 % in small rodents (Glazier 1985; Innes and Millar 1981) and by 54 % in lagomorphs (*Lepus europaeus* —Valencak et al. 2009). This reproductive strategy results in low investment of maternal energy that ends by early

summer and allows mothers to restore fat mass through most of the season of plant growth when food quality is high.

No evidence exists that porcupines reduce metabolic costs by lowering core body temperature on a daily or seasonal basis; Core body temperatures varied by only 1.5 °C daily. Therefore, porcupines must rely on behavioral and other physiological adaptations to meet high thermoregulatory demands in winter (DeMatteo and Harlow 1997; Oveson 1983; Po-Chedley and Shadle 1955; Roze 1987). DeMatteo and Harlow (1997) found that porcupines decrease skin and subcutaneous temperatures as ambient temperatures vary within their thermoneutral zone. In addition, regional heterothermy can reduce overall metabolic costs (Irving 1972). Behaviorally, porcupines reduce heat loss by piloerection of their fur and by pressing their quills against their skin in areas with little underfur, creating a significant boundary layer (DeMatteo and Harlow 1997). As a result, porcupines have a lower conductance than is predicted by their body size, which should reduce metabolic thermoregulatory costs (DeMatteo and Harlow 1997) regardless of any decrease in core body temperature. Furthermore, we suspect that porcupines in the northern limits of their range are acclimatized to a LCT <-11 °C, as estimated by DeMatteo and Harlolw (1997), because porcupines in our study were subjected to >100 days of ambient temperatures <-11 °C. Maintaining a LCT <-11 °C would allow for additional thermoregulatory savings.

Water turnover rates for both captive and free-ranging porcupines are extremely low compared to the mean for eutherian mammals (123 ml · kg^{-80} · d^{-1}—Richmond et al. 1962). However, water turnover rates based on lean mass are similar to whole body turnover rates for other arboreal folivores, assuming they possess similar lean body mass and minimal fat mass (Degabriel et al. 1978; Kennedy and Heinsohn 1974; Krockenberger 1993; Nagy and Montgomery 1980). Both free-ranging female koalas (*Phascolarctos cinereus*) and captive koalas have comparable winter water turnover rates (88 ml · $kg^{-0.71}$ · d^{-1} and 92.3 ml · kg^{-80} · d^{-1}, respectively—Degabriel et al. 1978; Krockenberger 1993). Low turnover rates in porcupines are both a reflection of water availability and use (Degabriel et al. 1978). During winter water is consumed as snow,

absorbed as preformed water in food (white spruce needles and cambium of white spruce and paper birch), and produced during metabolism (metabolic water production), while water is lost via evaporation, respiration, and in urine and feces. We saw no evidence that captive porcupines with significant water turnover rates ($n = 7$) were in osmotic stress based on osmotic concentrations of urine relative to plasma (U/P ratio; Coltrane and Barboza 2010; **CHAPTER 2**). These porcupines were given snow ad libitum and ingested 5 ± 1 g $\cdot$ $kg^{-0.75}$ of preformed water, which was equivalent to 17 % of daily water turnover. As snow provides relatively little water on a per volume basis (approximately 5 % water per snow volume at -12 °C), consumption of snow requires longer handling time than drinking water. However, the relatively slow intake rate of snow might decrease potential cold shock to ingesta and reduce energy demands compared to the consumption of cold water (Crater and Barboza 2007). Although snow is typically abundant and handling time might not be a limiting factor for porcupines, production of metabolic water most likely plays an important role in water intake, as oxidation of fat stores produces 1.07 g $H_2O \cdot g^{-1}$ fat. Based on daily fat loss of 12.78 ± 4.97 g $\cdot$ d^{-1}, free-ranging porcupines produced 13.67 ± 5.32 g $H_2O \cdot d^{-1}$, or 52 % of daily water turnover.

Fecal water loss was the most significant route of excretory water loss in captive porcupines. Insensible water loss in porcupines is probably low. Cutaneous water loss is minimized by maintaining a high boundary layer, and respiratory water loss is reduced when foraging by having lips behind the incisors, which allows porcupines to keep their mouths shut when scraping cambium from trees. In addition, nasal cooling most likely further reduces respiratory water. Therefore, a significant source of water intake for porcupines in winter is likely metabolic production, with fecal water loss being the highest contributor to overall water efflux. The slow rate of water turnover exhibited by wintering porcupines indicates lower energy use or FMR.

Estimated FMR for free-ranging porcupines was low compared to other eutherian herbivores (Nagy et al. 1999). Comparatively, the estimated FMR was only slightly higher than FMR recorded for koalas (388 kJ $\cdot$ $kg^{-0.734} \cdot d^{-1}$) and three-toed sloths (*Bradypus variegatus*; 209 kJ $kg^{-0.75} \cdot d^{-1}$), both arboreal folivores with similar ecological

niches to porcupines (Nagy and Montgomery 1980; Nagy et al. 1999). However, compared to koalas and sloths, porcupines are subjected to higher thermoregulatory demands in winter, and therefore, we would expect to see even higher FMR than estimated. On a lean mass basis, FMR was only 4.4 times the predicted basal metabolic rate based on body size (Kleiber 1947), and only 31 % lower than predicted FMR based on whole body mass ($4{,}130 \pm 613$ kJ $\cdot$ $kg^{-0.734}$ $\cdot$ d^{-1}—Nagy et al. 1999). The lower than predicted FMR for porcupines is most likely influenced by habitat, diet selection, thermoregulatory capacity, and phylogeny (Nagy et al. 1999). In general, metabolic rates for arboreal folivores are typically lower than predicted for their body mass (Arends and McNab 2001; McNab 1978, 1986) and consistent with the low maintenance requirements (398 kJ $\cdot$ $kg^{-0.75}$ $\cdot$ d^{-1}—Coltrane and Barboza 2010), slow water turnover rates, and low thermal conductance of porcupines.

Porcupines conserve lean body mass in winter by balancing the consumption of poor-quality forages with the use of fat stores. Fat losses are minimized by lowering rates of energy expenditure (i.e., FMR) and water turnover. Porcupines can use a wide variety of diets, but winter survival is dependent on food quality at the northern limits of their range. Although porcupines can readily switch foraging strategies from generalist to specialist herbivore (**CHAPTER 1**), consumption of forage high in PSM is not sustainable year round, because animals must replenish their stores of fat and protein for survival and reproduction in the following year.

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Table 3.1. Body, fat, and lean mass of free-ranging porcupines (n = 25) in Anchorage, Alaska. Values reported as means ± *SD*. Body mass, fat mass, and lean mass were compared among seasons using ANCOVA, with individual and date as covariates. Pairwise contrasts were performed with Bonferroni adjustments for multiple comparisons among periods. Different superscripts indicate significant differences among seasons for each body mass component ($P < 0.0125$).

Season	Body Mass (kg)			Fat Mass (kg)			Lean Mass (g)		
Fall	9.42	±	2.21^{A}	4.37	±	1.32^{A}	2.59	±	$0.5o^{A}$
Winter	6.6	±	1.83^{B}	1.92	±	1.33^{B}	2.96	±	0.69^{A}
Spring	6.25	±	1.56^{B}	1.77	±	1.10^{B}	2.85	±	1.22^{A}
Summer	7.76	±	1.78^{A}	2.95	±	0.92^{A}	2.95	±	0.92^{A}
ANCOVA	*F*	*d.f.*	*P*	*F*	*d.f.*	*P*	*F*	*d.f.*	*P*
Individual	7.18	24, 45	<0.0001	2.7	24, 45	0.0002	3.09	24, 43	<0.0001
Sex	11.82	1, 45	<0.0001	7.8	1, 45	0.0008			
Day	20.32	1, 45	<0.0001	35.41	1, 45	<0.0001	5.49	1, 43	0.024
Season	28.13	3,45	<0.0001	29.33	3, 45	<0.0001	1.09	3, 43	0.363

Table 3.2. Water turnover statistics for captive (n = 7) and wild (n = 10) porcupines during mid-winter in Anchorage and Fairbanks, Alaska. Slope represents the relationship between the natural log of deuterium in the sample and time from initial dosing. The intercept is the natural log of deuterium in the sample when time = 0.

	Captive	Wild
Body Mass (kg)	9.32 ± 2.27	7.17 ± 2.08
Lean Mass (kg)	2.41 ± 0.86	3.22 ± 0.79
Body Water Pool (kg)	2.82 ± 0.84	3.40 ± 0.81
Slope (K)	-0.055 ± 0.013	-0.034 ± 0.008
Intercept	-5.575 ± 0.092	-5.927 ± 0.092
Turnover Time (d)	19 ± 5	32 ± 10
Turnover Rate (ml · $kg^{-0.75}$ · d^{-1})	29 ± 8	26 ± 7
Turnover Rate (ml · $kg^{-0.75}$ lean mass · d^{-1})	81 ± 21	48 ± 12

Table 3.3. Estimated field metabolic rate (FMR) of wild, free-ranging porcupines during mid-winter (January) in Anchorage, Alaska.

Individual	Sex	Fall Body Mass (kg)	Fall Lean Mass (kg)	Maintenance Energy Requirement* ($kJ/kg^{0.75}/d$)	FMR ($kJ/kg^{0.75}/d$)	FMR based on Lean Body Mass ($kJ/kg^{0.75}/d$)
1	♀	9.26	2.21	2,113	469	1,373
2	♀	9.58	2.40	2,167	450	1,269
3	♀	7.14	2.36	1,738	425	974
4	♀	8.75	2.16	2,025	479	1,369
5	♀	7.6	1.83	1,822	481	1,399
6	♂	11.86	3.50	2,544	475	1,187
7	♂	13.24	3.09	2,762	484	1,442
8	♂	11.76	3.01	2,527	462	1284
9	♂	11.38	2.96	2,466	498	1,369
10	♂	8.96	2.86	2,061	449	1,058

* Maintenance energy intake at zero mass change in captive porcupines during winter (398 $kJ \cdot kg^{-0.75} \cdot d^{-1}$, Coltrane and Barboza 2010).

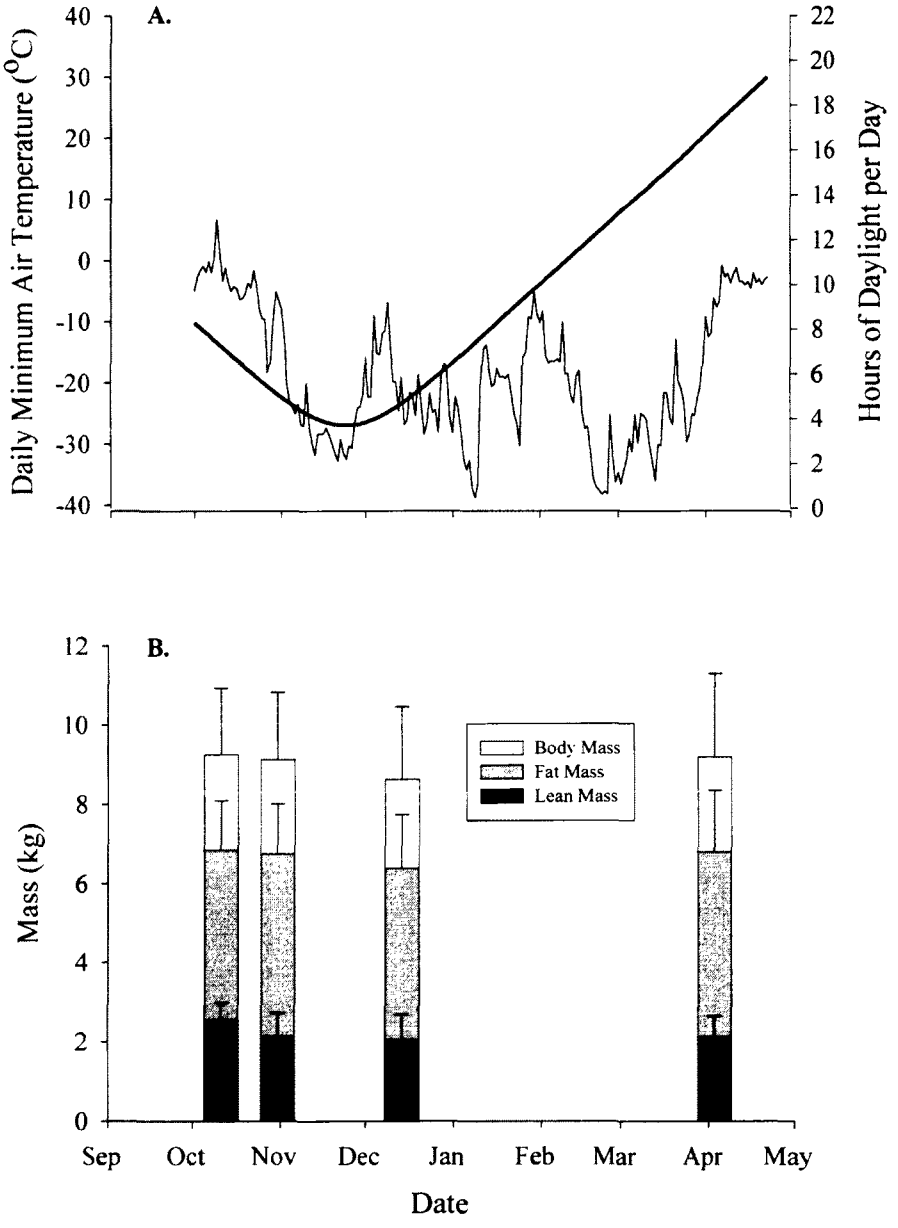

Figure 3.1. A) Daily minimum air temperatures (°C) and hours of daylight per day within captive porcupine enclosures in Fairbanks, Alaska, from October 2006 through April 2007. B) Average (+ *SD*) body mass, fat mass, and lean mass for captive porcupines in Fairbanks, Alaska during mid and late October (n = 10), December (n = 10) and early April (n = 9).

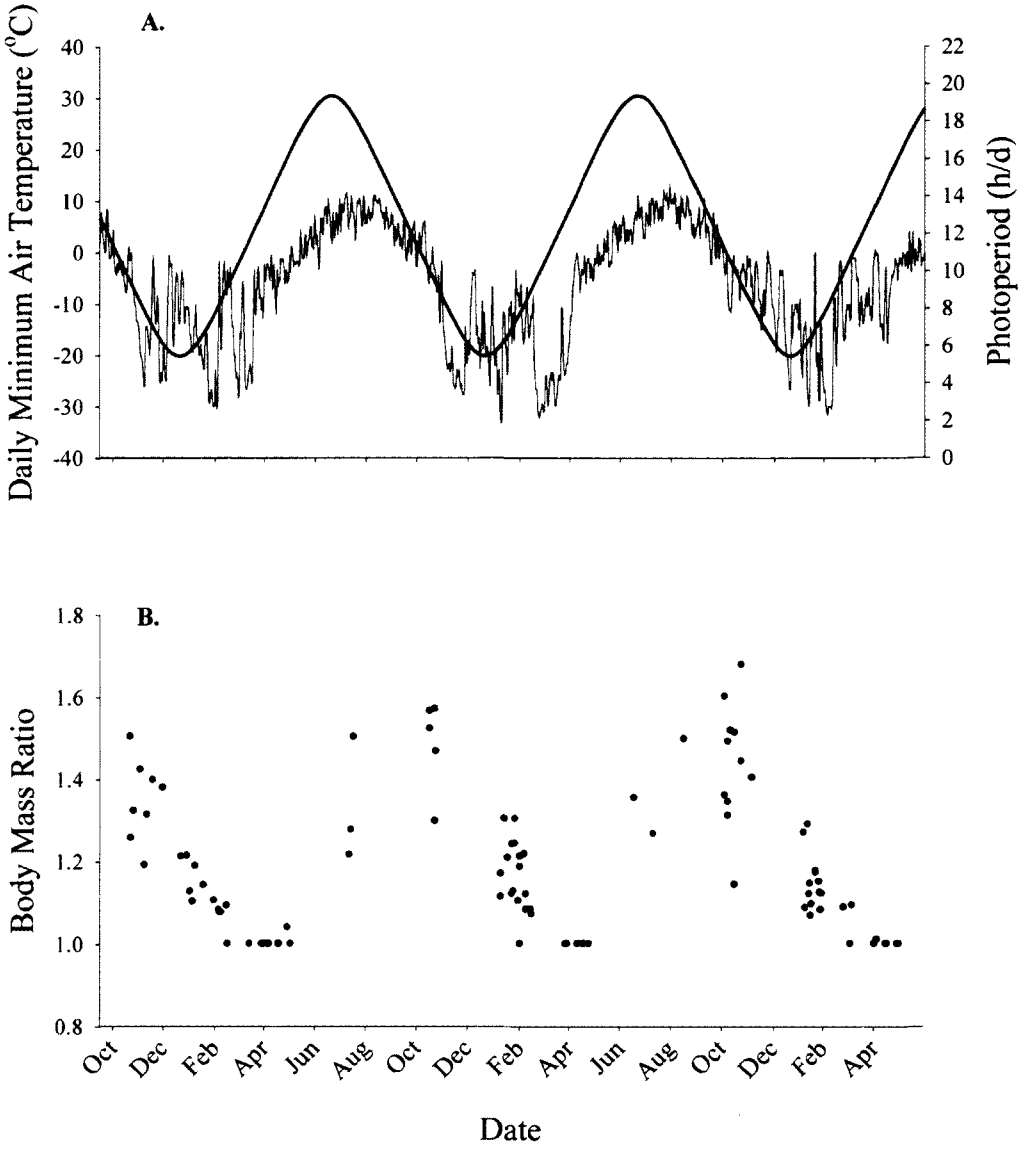

Figure 3.2. A) Daily minimum air temperatures (°C) and hours of daylight per day at the Campbell Creek Science Center in Anchorage, Alaska, from October 2005 through April 2008. B) Patterns of normalized body mass expressed as the ratio to minimum annual body mass of free-ranging porcupines in Anchorage, Alaska, from October 2005 through April 2008 (n = 19).

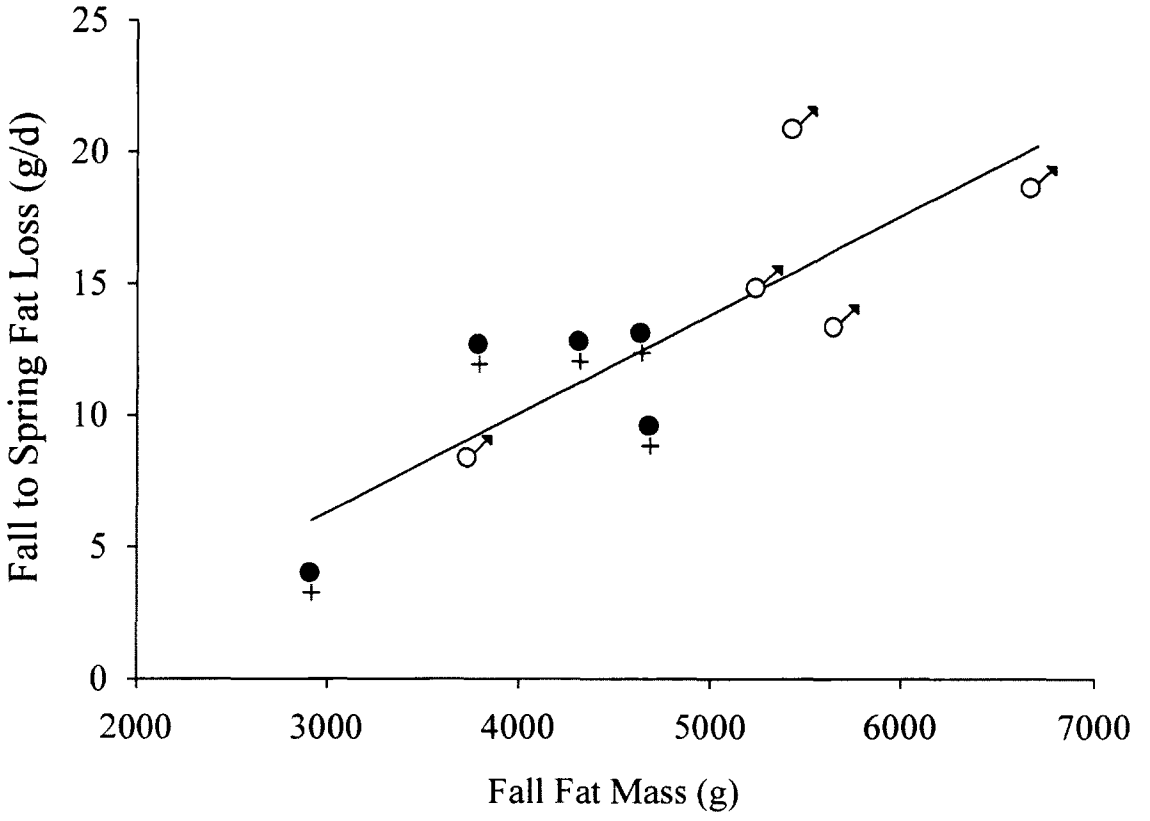

Figure 3.3. Comparison between fall fat mass (g) and winter (fall to spring) fat loss ($g \cdot d^{-1}$) for free-ranging porcupines ($n = 10$) in Anchorage, Alaska, from October 2005 through April 2008 ($Y = 0.004x - 4.93 \pm 2.93$, $R^2 = 0.691$).

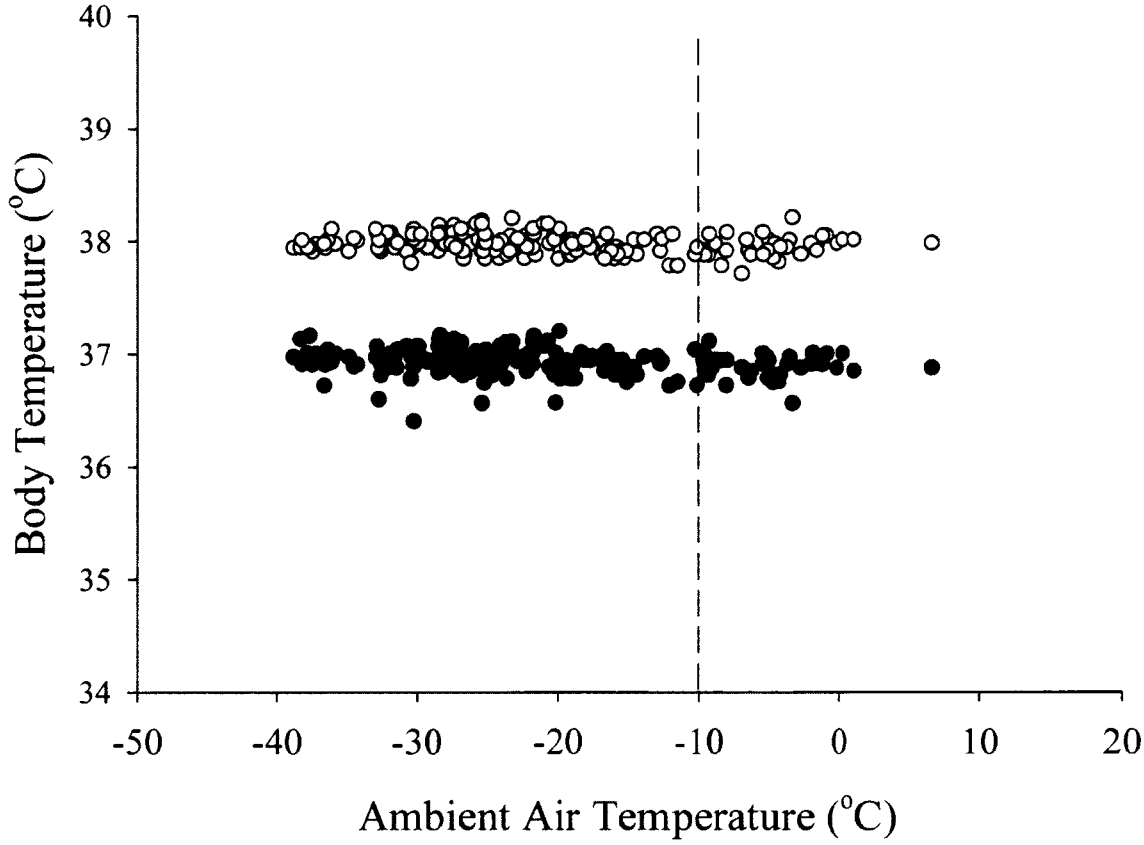

Figure 3.4. Average daily minimum and maximum body temperatures (°C) measured in the abdominal cavities of captive porcupines (n = 7) in Fairbanks, Alaska, from 1 October 2006 to 3 April 2007. The vertical line indicates the estimated lower critical temperature (LCT; -10 °C) for North American porcupines reported by DeMatteo and Harlow (1997).

CHAPTER 4 - WINTER HABITAT SELECTION OF NORTH AMERICAN PORCUPINES (*ERETHIZON DORSATUM*) AT THE NORTHERN LIMIT OF THEIR RANGE[a]

Abstract

Habitat selection results from trade-offs between availability and use of resources under constraints of predation, competition, or other threats, which can vary spatially and temporally. For northern herbivores, winter food availability and quality can limit population size and may drive habitat preference. North American porcupines (*Erethizon dorsatum*) are widespread generalist herbivores that range from Mexico to the northern reaches of Alaska. During the long Alaskan winter, porcupines deal with high energetic demands resulting from low ambient temperatures while subsisting on low quality forage. Habitat selection at the extremes of porcupine distribution may be restricted to patchily distributed suitable habitat, resulting in a higher degree of selectivity than observed for porcupines in the more temperate regions. We tracked free-ranging porcupines over 3 winters in southcentral Alaska to determine habitat selection and home range size in relation to diet. Porcupines maintained larger than expected home ranges and selected for conifer/hardwood forests at the home range level. Unfortunately, individual variation among porcupines was too large to determine microhabitat selection of tree use. Regardless, direct observations revealed that porcupines used only white spruce and paper birch trees for foraging. White spruce may provide some nutritional and thermoregulatory advantage over paper birch; however, porcupines did feed on paper birch cambium, suggesting some nutritional requirement is met by eating paper birch. Maintaining mixed conifer/hardwood forests in southcentral Alaska would provide suitable winter habitat for porcupines and may alleviate damage to single species stands of conifers or hardwoods, which are preferred by commercial forestry operations.

[a]Coltrane, J. A., and R. Sinnott. Winter habitat selection of North American porcupines (*Erethizon dorsatum*) at the northern limit of their range. *Prepared for submission* in Journal of Wildlife Management.

Introduction

Habitat selection is often the result of trade-offs between availability and use of resources under constraints of predation, competition, or other threats (Morris 2003). The relative importance of these factors can vary with spatial and temporal scales (Finlayson et al. 2008, Leiner et al. 2010). For example, annual and seasonal patterns of precipitation, ambient temperature, and predation may limit the regional distribution of herbivores, while vegetation and availability of cover from predation or environmental extremes may affect local distributions and densities (Leiner et al. 2010). In addition, habitat selection may vary among populations due to the distribution of quality and availability of resources over space and time (Boyce 2006). Presence and population densities of widespread species typically decrease from the center to the edge of their geographic range as habitat quality and other environmental factors become less suitable (Brown 1984). Therefore, populations at the edge of their range may be restricted to small patches of suitable habitat (Hampe and Petit 2005) and, as a result, these populations may exhibit a higher degree of habitat selectivity than their centrally located counterparts (Avila-Flores et al. 2010). For northern herbivores, winter food availability and quality can limit population size (White et al. 1987, Marchand 1996, Blix 2005) and may drive habitat preference.

North American porcupines (*Erethizon dorsatum*) are considered widespread generalist herbivores (Woods 1973) that range from Mexico to the northern reaches of Alaska where they occupy a diverse array of habitats from desert chaparral to temperate forests and arctic tundra (Dodge 1982). Porcupines are typically considered arboreal, using trees not only for food, but for refugia from low ambient temperatures (Roze 2009) and predators (Sweitzer 1996). Selection for forested habitats is more prevalent in winter when ground vegetation becomes unavailable and thermal demands increase (Dodge 1982, Roze 1984, 2009; Tenneson and Oring 1985, Habeck 1990, Griesemer et al. 1998). Coniferous trees provide abundant low quality leaves and offer some shelter from wind and reduce radiant heat loss (Clarke and Brander 1973; Roze 1987, 2009), whereas

deciduous trees provide food for porcupines, but little insulation in winter. Because porcupines preferably use deciduous trees over coniferous trees in some areas (see Roze 2009), deciduous trees may provide a nutritional advantage over coniferous trees (Stricklan et al. 1995). In addition, den availability and location influence winter habitat selection in some areas (Roze 1987, 2009; Griesemer et al. 1998). Dens vary from rocky outcroppings to hollow trees and root masses and provide porcupines with shelter from predators and inclement weather (Roze 1987, 2009; Griesemer et al. 1998).

Alaska is at the northern limit of the porcupine's range (Dodge 1982). Therefore, populations of Alaskan porcupines may be restricted to patchily distributed suitable habitat, resulting in a higher degree of habitat selectivity than is observed in populations at the center of their range (Avila-Flores et al. 2010). Survival of northern porcupine populations may ultimately depend on winter habitat availability and selection. During long Alaskan winters, porcupines endure low ambient temperatures while subsisting on poor quality foods that are high in plant secondary metabolites (PSM) and fiber and low in nutrients and energy (Coltrane and Barboza 2010; **CHAPTER 2**), as well as body stores (Coltrane et al. 2011; **CHAPTER 3**). Habitat selection in Alaskan porcupines in winter is therefore a tradeoff between nutritional and thermoregulatory challenges, as well as predation risks. As a result, free-ranging porcupines lose up to 34 % of total body mass at an average rate of 17 ± 6 g $\cdot$ d^{-1} over an Alaskan winter (Coltrane et al. 2011; **CHAPTER 3**). Captive porcupines fed a diet of white spruce needles lost body mass at 49 $\pm$ 19 g $\cdot$ d^{-1} (Coltrane and Barboza 2010; **CHAPTER 2**), a loss rate that could not be sustained throughout the winter. However, porcupines can readily regain body mass by consuming higher quality forage when available (Coltrane and Barboza 2010; **CHAPTER 2**). As a result, we suspect that porcupines select habitats that allow for the ability to switch between several food items, such as coniferous to deciduous trees, when toxin loads or energy loss exceed an internal threshold (Wiggins et al. 2006). Furthermore, porcupines should select for habitats that provide refugia to help alleviate thermal demands and predation risks.

We tracked free-ranging porcupines over 3 winters in south central Alaska to determine habitat selection and home range size in relation to diet. We hypothesized that home ranges of porcupines in Alaska would be larger than reported for porcupines in more temperate areas due to decreased diet quality and increased average body size of Alaskan porcupines. In addition, we expected porcupines to select for mixed coniferous/deciduous forests within their home ranges, so that diet switching could be easily facilitated. We also hypothesized that porcupines would favor thermal cover in coniferous trees and dens especially when ambient temperatures fell below the estimated lower critical temperature (LCT) for porcupines of 11° C (DeMatteo and Harlow 1997). We also expected den use to be more prevalent in smaller-bodied porcupines, which should have lower surface to volume ratios and a higher rate of heat loss than larger-bodied individuals (Marchand 1996) and may be more susceptible to predation (Sweitzer and Berger 1992).

Methods

Study Area

This study was conducted in the Municipality of Anchorage, Alaska (5079 km^2; 61.17° N, 150.02° W). Anchorage is a mix of urbanized areas interspersed with a patchwork of natural habitat fragments that is bounded to the east by a 2023 km^2 state park (Chugach State Park). Field work was focused in Far North Bicentennial Park (a 16 km^2 municipal park), Campbell Tract (a 3 km^2 park managed by the Bureau of Land Management), and adjacent state park lands (Fig. 4.1). The study area was bounded to the north, west and south by urban areas, while the eastern boundary was delineated by locations of radio collared porcupines. The study area included 37 km^2 of natural habitat and a small residential neighborhood typified by large parcels and native vegetation. Five stream corridors, with numerous smaller tributaries, were located in the study area. Average ambient air temperatures were recorded daily at the Campbell Creek Science Center, Anchorage, located within the study area (N 61° 09.843', W 149° 46.625').

Animal Captures

All procedures and handling protocols were approved by the Institutional Animal Care and Use Committee, University of Alaska Fairbanks (UAF; protocol 06-027) and were consistent with guidelines approved by the American Society of Mammalogists (Sikes et al. 2011). We captured 19 porcupines (11 females and 8 males) between August 2005 and January 2008 using nets or live traps in the study area. Porcupines were transported to a laboratory and immobilized with Telazol (Tiletamine HCl and Zolazepam HCl; $5g \cdot kg^{-1}$) injected intramuscularly into the base of the tail. Porcupines were then fitted with a very high frequency (VHF) radio collar (model 225, Telonics, Inc., Mesa, Arizona) and marked with a unique identification tattoo on the skin of the lower abdomen. Individuals were weighed (± 0.01 kg, AE Adams CPW Plus 35, Adam Equipment Inc. Danbury, CT) and classified as sub-adults or adults (> 2 years) based on tooth eruption patterns and body mass (adults: > 5 kg; Dodge 1982). Porcupines were held for up to 12 hours to ensure complete recovery from immobilization before they were released at the capture site or within Far North Bicentennial Park (61.15° N, 149.75°W) in Anchorage.

Radio Telemetry and Home Range Analysis

Porcupines were relocated via radio telemetry as frequently as possible during the fall (September through October), mid-winter (November through March), and spring (April through May) from fall 2005 through spring 2008. Radiolocations were assumed independent if they were separated by at least 24 hours. Porcupines tended to travel from one location to the next overnight, and could traverse up to 2.5 km over a 24 hour period. We located each porcupine visually and recorded latitude and longitude using a portable global positioning system unit (GPS; Garmin eTrex Venture, Garmin, Kansas City, Kansas). In addition, we recorded time of day, ambient air temperature, description of location (including den type or tree species), and any signs of feeding activity. Porcupine activity and causes of mortality were also recorded when possible.

Home ranges were calculated annually for porcupines from fall through spring using the fixed kernel density estimator (KDE) of Hawths Tools extension in ArcGIS 9.3.1with a 500 m bandwidth at 95 %, 90 %, and 50 % isopleths. We also calculated home ranges using minimum convex polygon estimator (MCP) of Hawths Tools extension in ArcGIS 9.3.1, so that we could directly compare our results with those of previous studies using MCP analysis. We tested parametric assumptions of normality using Shapiro-Wilk test, and we used Levene's test to determine if variances were normally homogenous. Home range size of porcupines was compared among winter periods using analysis of variance (ANOVA, F). We compared home range size between males and females for all years combined with a 2-sample t-test.

Chemical Analysis of Forage

Samples of white spruce (needles and cambium) and paper birch cambium were collected randomly at feeding trees from October through January to compare nutritional content of forage items. Samples were dried at 55 °C in a fan-forced oven to a constant mass to determine dry matter (DM) content. Cambium samples were ground through #20 (1.25 mm) screen in a Wiley Mill. White spruce needles were ground in the same manner, but with dry ice (solid CO_2) to prevent separation of resins in the mill.

We used an elemental analyzer (CNS2000, LECO, St. Joseph, MI) to determine N content, which was converted to organic matter in crude protein at 6.25 g organic matter$\cdot g^{-1}$ N in (Robbins 1993, Van Soest 1994). Fiber was analyzed by detergent extraction (Van Soest et al. 1991) in polyester bags (F57 bags, Ankom, Macedon, NY). Neutral detergent fiber (NDF) was extracted with thermo-stable amylase (Ankom) to dissolve starches, and with sodium sulfite to denature structural proteins. We assumed that the neutral detergent procedure dissolved crude protein, lipids and non-structural carbohydrates (e.g., sugars, starches, pectins).

Total phenols were determined using the method described by Singleton et al. (1999). Samples were first extracted with acetone, and then diluted with deionized water, Folin-Ciocalteau Reagent (Sigma-Aldrich Catalog # F9252-1L) and 20 % sodium

carbonate solution. Absorbance was measured at 765 nm in a spectrophotometer (Beckman DU 530, Fullerton, CA). Total phenols were calculated as equivalents of gallic acid and reported as mmol·100 g DM^{-1}. We tested parametric assumptions of normality using Shapiro-Wilk test, and we used Levene's test to determine if variances were normally homogenous. Forage components were compared using 2-sample *t*-tests with pooled variances.

Habitat Selection

We categorized habitat within the study area using geographical information system (GIS) coverage of vegetation classes (Viereck et al. 1992) produced by Geographic Resource Solutions (Anchorage, Alaska) for the Municipality of Anchorage Fire Department between 2004 and 2007. This coverage was generated using Landsat ETM imagery verified by ground and photo plots with a resolution of 30 m per pixel. The study area was categorized into 20 vegetation types, including one unknown category (Table 4.1). We quantified habitat selection for winter across all years on two scales: microhabitat and home range. Microhabitat selection was defined as the frequency of use for each tree species by individual. We used a log linear model to assess patterns of tree use among individual porcupines during the winter periods (R version 2.12.2, The R Foundation for Statistical Consulting). We used Fisher's Exact Test to examine differences in the use of feeding trees by sex (Zar 1999).

At the home range level, use was measured as the proportion of animal observations within each available vegetation type in individual home ranges across all winters combined (Manly et al. 2002). For this analysis, we combined vegetation types into 10 vegetation categories. We evaluated use of combined vegetation categories by individual porcupines with selection ratios and standardized selectivity indices and their 95 % confidence intervals (Manly et al. 1993). Selection ratios were calculated by averaging a measure of use in each habitat and the proportion of each habitat available. Selection ratios were reported with the standard error of the mean. Significant differences of selection ratios from 1.0 were determined using a *z*-score. Comparisons of

selection ratios were made using a 2-sample *t*-test. Pairwise contrasts were performed with Bonferroni adjustments for multiple comparisons among selection ratios. We used Pearson's χ^2 Test to examine differences in the use of vegetation types by individual porcupines and to compare sexes (Zar 1999). The average proportion of use of each vegetation category was estimated using a ratio of means. Statistical analyses were executed with modules in SYSTAT 11 (SYSTAT Software, Richmond, Calif.) and R (version 2.12.2, The R Foundation for Statistical Consulting). Statistical significance was determined as $\alpha < 0.05$. Standard errors of means (*SE*) are reported for selection ratios. Means (± *SD*) are reported for all other values.

Results

Porcupine Locations and Home Range Size

We observed 19 porcupines from August 2005 through April 2008. Each animal was relocated between 6 and 77 times, for an average of 29 ± 20 relocations per animal. Most relocations (366 of 499) were in mid-winter with 81 and 52 relocations in spring and fall, respectively.

We determined winter home ranges using KDE for 10 porcupines (4 males and 6 females) in 2005-2006, 8 porcupines (3males and 5 females) in 2006-2007, and 13 porcupines in 2007-2008 (5 males and 8 females; Table 4.2). There was no difference in home range sizes (KDE 95 % isopleth) among the winter periods of 2005-2006 (0.89 ± 0.23 km^2), 2006-2007 (1.06 ± 0.32 km^2), and 2007-2008 (1.00 ± 0.40 km^2; $F_{2,16} = 0.432$, $P = 0.657$). Average home range size for all years combined was 0.98 ± 0.33 km^2 at the 95 % isopleth, 0.72 ± 0.25 km^2 at the 90 % isopleth, and 0.25 ± 0.07 km^2 at the 50 % isopleth ($n = 32$). Because no variation among winters was detected, all additional analyses were conducted using home ranges for all years combined and the KDE 95 % isopleth. While home ranges were slightly larger in males (1.11 ± 0.38 km^2) than in females (0.89 ± 0.26 km^2) for all winter periods combined (Table 4.2), this difference was not significant ($t_{17.7} = -1.77$, $P = 0.094$). Male porcupines were slightly larger than females; however, there was no difference in mean fall body mass between sexes ($t_{8.7} = -$

1.514, $P = 0.165$). In addition, there was no relationship between maximum fall body mass and home range size ($Y = 0.799x + 7.511 \pm 2.472$, $R^2 = 0.026$, $P = 0.506$). Average home range size for all porcupines based on the MCP method was 1.71 ± 2.30 km^2 (0.94 ± 1.64 km^2 for females and 2.77 ± 2.75 km^2 for males).

Porcupine Habitat Selection and Forage Analyses

Vegetation types were combined into 10 categories that were used to determine habitat selection at the home range level (KDE estimates; Table 4.3). We used only porcupines with ≥ 20 locations for the analysis of habitat selection ($n = 14$ porcupines). Both males ($n = 7$, $\chi^2_{63} = 262.792$, $P < 0.0001$) and females ($n = 7$; $\chi^2_{63} = 283.977$, $P < 0.0001$) used habitat disproportionately to the available area within their home ranges (both sexes combined: $\chi^2_{126} = 546.770$, $P < 0.0001$). Porcupines avoided barrens, black spruce, shrub, and white spruce habitats; selection ratios were significantly less than 1.0 ($P < 0.0035$) for these vegetation types (Table 4.3). These habitat types comprised 1.6 ± 2.9 %, 8.3 ± 7.5 %, 4.4 ± 4.0 %, and 9.4 ± 5.5 % of all home ranges, respectively (an average of 24 % of all home ranges combined). Porcupines selected mixed conifer/hardwood forest over black spruce ($P = 0.004$), bluejoint meadow ($P = 0.000$), and shrub ($P = 0.003$). While there was some evidence of selection of mixed conifer/hardwood forests over white spruce, this relationship was not significant at $\alpha = 0.005$ based on a Bonferroni correction for multiple comparisons.

Micro-habitat selection was documented for 19 porcupines (11 females and 8 males). We observed porcupines primarily in cottonwood (*Populus balsamifera*), paper birch (*Betula papyrifera*), and white spruce (*Picea glauca*) trees (87 % of total locations; Table 4.4). Porcupines were observed in white spruce more than paper birch and cottonwood trees during the winter period (80 % of observations in all trees; Table 4.4). However, individual variation in tree species use was large for both males ($\chi^2_{14} = 97.572$, $P < 0.0001$) and females ($\chi^2_{20} = 84.189$, $P < 0.0001$; Table 4.5). Therefore, no significant patterns of selection among tree species could be determined.

During the winter period, we did not observe any feeding activity or evidence of feeding by porcupines on cottonwood trees. Hence, we considered that during the winter period porcupines were not feeding in cottonwood trees, but were simply using them as temporary roosting sites. In comparison, we frequently observed porcupines feeding in white spruce and paper birch; thus, we considered white spruce and paper birch to be the only available forage tree species during winter.

Porcupines were observed eating paper birch cambium, as well as white spruce needles and cambium. White spruce needles contained slightly more N than white spruce cambium (t_{10} = -2.887, $P < 0.016$, Table 4.6), while C content did not vary between white spruce needles and cambium (t_{10} = -0.651, $P = 0.530$, Table 4.6). However, phenol concentration in white spruce cambium was greater than in white spruce needles (t_{10} = 11.108, $P < 0.000$). Only one vegetation sample was obtained for birch cambium, so no statistical comparisons could be made between birch cambium and other forage items. However, N content of birch cambium was more similar to that found in white spruce needles, and C content was similar to both white spruce cambium and needles (Table 4.6). Birch cambium was higher in phenol concentration than both white spruce cambium and needles.

Comparing forage tree species only, porcupines were observed more often in white spruce than paper birch (79 % vs. 21 % of observations), with no difference between sexes ($\chi^2_1 = 0.201$, $P = 0.713$). However, variation of feeding tree use by individual porcupines was significant for males ($\chi^2_7 = 81.198$, $P < 0.0001$) and females ($\chi^2_{10} = 52.199$, $P < 0.0001$; Table 4.5). As a result, no pattern of forage tree use across individuals could be determined.

Porcupines were observed using trees at different frequencies during the winter period (Figure 4.2). We observed porcupines in spruce trees more frequently than in birch trees during fall and mid-winter, while porcupines were observed in white spruce and paper birch at the same frequency during spring.

There was no clear pattern of den use by porcupines during winter in our study area. We observed twelve porcupines (6 males and 6 females) using den sites on 49 of

498 occasions (10 % of total observations; Table 4.4). Porcupines used dens at minimum daily ambient temperatures ranging from -33 to +11 °C.

Porcupine Activity and Mortality

We recorded porcupine activity at 363 locations during the winter period (Figure 4.3). The majority of observations (60 %) were of porcupines resting in trees, followed by porcupines feeding in trees (23%).

Four porcupines (3 males and 1 female) died during the study. However, only 1 mortality (1 male) was attributed to predation, either by a lynx (*Lynx canadensis*) or a coyote (*Canis latrans*). One male was killed by a human, and 1 female was found dead in her den, of what appeared to be starvation. An additional male died after immobilization, which was likely a combined effect of the immobilization drug and poor body condition. All porcupine deaths occurred during the summer or in the spring and therefore should have no impact on the analysis of winter home range size.

Discussion

Home Range Size

Porcupine winter home range size (0.98 ± 0.33 km^2, 95 % isopleth KDE and 1.71 ±2.30 km^2, MCP) was larger than expected based on reported home ranges for porcupines in more temperate habitats (Craig and Keller 1986, Zimmerling and Croft 2001). Average winter home range of adult porcupines was 0.0010 ± 0.0011 km^2 in an Idaho scrub desert (Craig and Keller 1986), while home range size was 0.0014 to 0.058 km^2, with a mean of 0.0153 km^2, in second growth forests dominated by western hemlock (*Tsuga heterophylla*) in British Columbia, Canada (Zimmerling and Croft 2001). In a north central Utah brush forest with mixed conifers and hardwoods, porcupine home ranges were 0.068 km^2 to 0.618 km^2. In comparison, home ranges varied from 0.074 ± 0.060 km^2 to .599 ± .940 km^2 between winters in the Catskill Mountains of New York (Roze 1987). Differences in home range size among study sites are most likely influenced by snow cover, den use, predation risks, and available forage

(Dodge 1982, Roze 1987, 2009; Sweitzer 1996, Zimmerling and Croft 2001). The extent to which these factors influence movements and therefore home ranges varies among habitats and age classes of porcupines. The relatively large home ranges in our study area are most likely a result of patchy distribution of preferred forage or roost trees, low availability or unavailability of den sites, low predation risk and larger body size of Alaskan porcupines compared to those at lower latitudes (Sweitzer and Berger 1993, Roze 2009).

Snow depth and density may influence home range size by impeding or facilitating porcupine mobility (Smith 1979, Roze 1987). Roze (1987) attributed the increase in home range size between winters in the Catskills to a 35 % reduction in snowfall, which facilitated easier ground travel. Average daily snow depth in our study area ranged from 35 ± 15 cm in 2005/2006 to 50 ± 26 cm in 2006/2007 and 24 ± 17 cm in 2007/2008. However, we did not measure snow density and hardness, which may influence a porcupine's mobility greater than snow depth alone. Therefore, we cannot evaluate the impact of snow on porcupine movement in relation to home range size. Regardless, porcupines in our study were on average larger than those found in the Catskills (Roze 2009). Male and female porcupines in our study area had average fall body masses of 10.62 ± 1.92 kg and 7.80 ± 1.68 kg, respectively (Coltrane et al. 2011; **CHAPTER 3**), compared to 5.53 kg and 4.59 kg for males and females, respectively, in the Catskill Mountains (Roze 2009). The larger body size of Alaskan porcupines may lessen the influence of snow depth on movement, at least at the relatively shallow depths typical of the study area. In addition, the longer winter experienced in Alaska relative to lower latitudes may require increased movements to exploit food resources within their home ranges.

Den site availability and location in relation to feeding trees can significantly influence daily movements of porcupines in temperate forested areas (Speer and Dilworth 1978, Roze 1987, Griesemer et al. 1994, Zimmerling and Croft 2001). Both Griesemer et al. (1994) and Roze (1987) found that porcupine feeding occurred close to winter dens (within 40 m and 30 m, respectively). Our study did not reveal any pattern of den use

among porcupines and the limited use of dens observed may allow increased movements and thus larger home ranges.

There was no indication that predation risks impacted home range size or movement of porcupines in our study area. During the 3-year study, only 1 porcupine was lost due to predation, and this event occurred in the summer. However, in other habitats predation can significantly influence movement patterns and habitat use of porcupines of varying age classes and size (Sweitzer and Berger 1992). In the Great Basin Desert, larger porcupines tended to travel greater distances and utilize habitat with less cover but higher nutritional value (risky predation behavior) compared to smaller porcupines that were more vulnerable to predation (Sweitzer and Berger 1992). Alaskan porcupines are on average larger than those found in lower latitudes (Sweitzer and Berger 1992, Griesemer et al. 1998, Zimmerling and Croft 2001, Roze 2009), which may partially account for the increased home range size observed in Alaska. However, within our study area, there was no indication that body size influenced movement in wintering porcupine; overall, fall body mass did not influence home range size of porcupines in our study area.

Sample size and the use of different home range metrics can dramatically alter estimations of home range size. In general, home range size increases and variability among mean home range estimates decreases with sample size (Bekoff and Mech 1984). However, small-bodied species typically have smaller home ranges that can be estimated with smaller numbers of animals (Harestad and Bunnell 1979, Bekoff and Mech 1984). In addition, the type of analysis used to estimate home range affects estimated size. Previous estimations of porcupine home ranges used minimum convex polygons (MCP) (Roze 1987, 2009; Sweitzer 1996, Zimmerling and Croft 2001). MCP, while simple to construct, often overestimate home range when sample sizes are large and underestimate home range when sample sizes are small (Bekoff and Mech 1984, Burgman and Fox 2003, Downs and Horner 2007). In addition, the MCP method provides no measure of internal home range space use and often contains large portions of unused space if the

estimated home range is not convex in shape (Worton 1989, 1987; Downs and Horner 2007).

In comparison to the MCP, the KDE, while a widely accepted method, is very sensitive to bandwidth selection (Kernohaen et al. 2001). While accuracy of KDE estimates typically improve with sample size, point pattern shape can dramatically alter the estimate of core home range when using an adaptive KDE (Downs and Horner 2007). We chose to use a fixed KDE with a 500 m bandwidth to estimate home range size, which has been shown to be more accurate than adaptive KDE methods (Seaman and Powell 1996). Although the fixed KDE method is robust and generally unbiased compared to MCP, it has been recommended that use of the 95 % isopleth should be avoided (Borger et al. 2006). Instead, Borger et al. (2006) recommend using the 90 % and 50 % isopleths for more accurate home range estimates. While it is possible that the 95 % isopleth over-estimates home range size for porcupines in our study area, we felt that due to small sample sizes of location data and high variation in sampling frequency, home range estimates using a 500 m bandwidth and a 95 % isopleth covered all potential winter movements by individual porcupines. However, porcupines tend to use specific core areas related to individual feeding trees and/or dens within their home range and have relatively small daily movements (Roze 1987, Sweitzer and Berger 1992, Griesemer et al. 1994). Therefore use of the 50 % isopleth may be a more accurate reflection of winter home range size (0.25 ± 0.07 km^2), which is similar to what was found for porcupines in the Catskill Mountains (Roze 1987, 2009). In comparison, MCP analysis appeared to overestimate large home ranges and underestimate small home ranges in our study area, resulting in large variances. Therefore we recommend the use of KDE to more accurately estimate home range size of porcupines.

Understanding site specific daily movement rates for individual porcupines would help increase the accuracy of home range estimates. However, our sampling regime did not allow for the collection of this type of data. Regardless, it seems clear that porcupines in our study area utilized larger home ranges than in more temperate regions

of their range, which is most likely a reflection of habitat availability or quality, as well as larger body size.

Habitat Selection

Our hypothesis that porcupines would select for mixed conifer/hardwood forests within their home ranges was supported by our data. While we did not find any specific selection for mixed forest types, porcupines selected against some habitats dominated by single species including barren, black spruce, shrub, and white spruce. Furthermore, a comparison among all habitat types indicated that porcupines selected mixed conifer/hardwood forests over black spruce, bluejoint meadow and shrub habitats. The weak relationship observed between white spruce and mixed conifer/hardwood forest is most likely a result of low sample size for some individual porcupines. However the use of mixed forests over white spruce dominated forests suggests that white spruce alone may not satisfy winter nutritional requirements of porcupines, regardless of thermoregulatory advantage that coniferous trees likely provide. These results concur with those of Morin et al. (2005), who found that porcupines selected for mixed forest over aspen dominated mixed forest and single species conifer forest types.

Unfortunately, variation in tree use among individual porcupines was too large to ascertain any statistically relevant pattern of microhabitat selection in our study area. However, direct observations revealed that porcupines used two forage tree species during winter, and most observations of porcupines were in white spruce trees. It is possible that white spruce needles may have provided a slight nutritional advantage over paper birch, since white spruce needles were higher in nitrogen and lower in total phenols than other dietary items. However, our nutritional analysis was limited, and we recommend additional component analyses to better understand the role of nutrition in habitat selection. The use of white spruce as forage and roosting trees may have provided a higher thermoregulatory advantage over paper birch trees (Clarke and Brander 1973, Roze 1989, 2009). During an Alaskan winter, thermoregulatory demands are high and the use of dens and coniferous trees should protect against radiant and convective

heat loss. Den use was infrequent in our study area and did not appear to be related to porcupine size or ambient temperature. However, Alaskan porcupines may be less dependent on dens than smaller porcupines from more temperate regions because lower critical temperature may be lower in Alaskan animals (DeMatteo and Harlow 1997, Coltrane and Barboza 2010), and because potential den sites may be less abundant or less accessible in Alaska (Morin et al. 2005, Roze 1987, 2009). As a result, white spruce trees may provide refugia for Alaskan porcupines that are similar to the thermal refugia provided by dens for porcupines in other locations (Roze 2009).

Regardless of potential nutritional or thermoregulatory advantages provided by white spruce trees, porcupines were observed in paper birch trees during winter. Since deciduous trees should not provide a thermal advantage during winter, it is likely that a nutritional requirement is met by paper birch cambium. Captive porcupines fed white spruce needles decreased dry matter intake (DMI) by 70 % over the course of the winter, as compared to a 43 % decline in DMI seen in porcupines fed a diet free of PSM (Coltrane and Barboza 2010; **CHAPTER 2**). These results suggest that intake of white spruce needles is limited by the rate that porcupines can detoxify PSM (Coltrane and Barboza 2010; **CHAPTER 2**). Switching to a diet of paper birch cambium may allow porcupines to increase intake by varying detoxification pathways for different PSM (Freeland and Janzen 1974, Dearing et al. 2005). The longest we observed a porcupine at one location was 19 days. During this time period, the porcupine was able to remain in the canopy and access both paper birch and white spruce, allowing for diet mixing.

Management Implications

Porcupines have been characterized as pests throughout most of their range by commercial forestry operations (Krefting et al. 1964, Storm and Halvorson 1967, Tenneson and Oring 1985, Sullivan et al. 1986). As a result, most studies have examined the effect of porcupine feeding on tree growth and survival or factors that contribute to forage selection by examining forage trees (Storm and Halvorson 1967, Sullivan et al. 1986). Few have focused on actual porcupine behavior (Tenneson and Oring 1985). An

understanding of regional, individual and seasonal variation in habitat selection on landscape and microhabitat scales is often absent, yet is paramount to designing effective management strategies to predict and reduce porcupine damage.

Our study indicates that porcupines maintain large winter home ranges that are dominated by mixed conifer/hardwood forests in southcentral Alaska and avoid single species stands of deciduous or hardwood trees, which are typically targeted for commercial harvest. However, porcupines are incredibly adaptable herbivores, as demonstrated by the wide array of habitats that they occupy throughout North America, as well as by recent northward and southward range expansions (Spencer 1964, Payette 1987, Ilse and Hellgren 2001). Their ability to occupy novel habitats suggests that porcupines may be able to expand to single species forest stands in southcentral Alaska if preferred mixed conifer/hardwood stands are unavailable. Maintaining mixed forests would provide suitable winter habitat for porcupines and may alleviate damage to single species stands of conifers or hardwoods that are preferred by commercial forestry operations.

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Table 4.1. Percent area of vegetation types within the study area (Anchorage, Alaska). Coverage of vegetation classes (Viereck et al 1992) produced by Geographic Resource Solutions using Landsat ETM imagery verified by ground and photo plots with a resolution of 30 m per pixel.

Vegetation Type	% Area
Barren	2
Paper Birch (*Betula papyrifera*): 60-100% canopy	24
Black Spruce (*Picea mariana*): 60-100% canopy	5
Black Spruce: 25-60% canopy	2
Black Spruce: 10-25% canopy	3
Bluejoint Meadow (*Calamagrostis canadensis*)	1
Western Hemlock (*Tsuga heterophylla*): 60-100% canopy	3
Mixed Conifer/Hardwood Forest: white spruce (*Picea glauca*), paper birch, black cottonwood (*Populus balsamifera*), 60-100% canopy	20
Mixed Conifer/Hardwood Forest: 25-60% canopy	5
Mixed Conifer/ Hardwood Forest: 10-25% canopy	1
Mixed Hardwood Forest: paper birch, black cottonwood, 25-60% canopy	2
Black Cottonwood: 25-60% canopy	1
Shrub: 60-100% canopy	1
Shrub: 25-60% canopy	6
White Spruce/Western Hemlock: 60-100% canopy	1
White Spruce: 60-100% canopy	4
White Spruce: 25-60% canopy	6
White Spruce: 10-25% canopy	1
Tall Shrub: willows (*Salix spp.*), alder (*Alnus crispa*), 60-100% canopy	8
Tall Shrub: willows, alder, 25-60% canopy	5
Unknown	1

Table 4.2. Winter home range size (mean ± *SD* km^2) and sample size (n) for male and female porcupines based on 95 %, 90 %, and 50 % kernel density estimate contours (500 m bandwidth) in Anchorage, Alaska.

			KDE Area (km^2)		
Winter	Sex	n	95 %	90 %	50 %
2005-2006	female	6	0.83 ± 0.16	0.67 ± 0.13	0.23 ± 0.04
2005-2006	male	4	0.99 ± 0.30	0.76 ± 0.20	0.22 ± 0.03
2006-2007	female	5	0.87 ± 0.22	0.73 ± 0.20	0.25 ± 0.08
2006-2007	male	3	1.37 ± 0.07	1.10 ± 0.09	0.35 ± 0.05
2007-2008	female	8	0.96 ± 0.40	0.77 ± 0.25	0.24 ± 0.07
2007-2008	male	5	1.06 ± 0.51	0.85 ± 0.41	0.28 ± 0.09
all winters combined	female	19	0.89 ± 0.26	0.73 ± 0.20	0.24 ± 0.06
all winters combined	male	13	1.11 ± 0.38	0.89 ± 0.31	0.28 ± 0.08

Table 4.3. Ratio of means, selection ratio, standardized selection index, 95 % confidence intervals, and *P*-values for selection of vegetation categories by porcupines ($n = 14$). Significance of selection ratios is established at as $P < 0.005$, due to Bonferroni correction for multiple comparisons.

Vegetation Category	Ratio of Means	Selection Ratio	SE	Standardized Selection Index	CI Lower	CI Upper	*Z*-score	two tailed *P*-value
Mixed conifer/hardwood	0.326	1.270	0.256	0.145	0.560	1.980	1.055	0.2915
Barren	0.015	0.255	0.255	0.029	0.000	0.962	-2.923	0.0035
Paper birch : 60-100% canopy	0.476	1.996	0.643	0.228	0.213	3.780	1.549	0.1214
Black Spruce	0.030	0.427	0.147	0.049	0.020	0.834	-3.902	0.0001
Bluejoint meadow	0.000	0.000	0.000	0.000	0.000	0.000		
Western hemlock: 60-100% canopy	0.028	0.792	0.540	0.090	0.000	2.288	-0.386	0.6994
Mixed hardwood forest	0.017	1.420	0.725	0.162	0.000	3.430	0.580	0.5622
Shrub	0.017	0.320	0.188	0.037	0.000	0.841	-3.616	0.0003
White Spruce	0.049	0.443	0.152	0.051	0.022	0.865	-3.664	0.0002
Tall Shrub	0.101	1.831	0.556	0.209	0.288	3.374	1.493	0.1353

Table 4.4. Number of observations of male and female porcupines at each location type during the winter period in Anchorage, Alaska.

Location	Male	Female	Total
Hemlock	6	1	7
Paper Birch	51	35	86
White Spruce	180	135	315
Cottonwood	16	17	33
Dead Tree	3	3	6
Den	12	37	49
Ground	0	2	2

Table 4.5. Distribution (%) of porcupine observations in white spruce, cottonwood, and paper birch trees during the winter period in Anchorage, Alaska.

ID Number	Sex	White Spruce	Cottonwood	Paper Birch	Total Observations
31	f	25	0	75	12
7	f	84	13	3	32
15	f	33	0	67	12
33	f	100	0	0	6
3	f	78	22	0	9
32	f	94	6	0	17
5	f	79	0	21	52
10	f	50	29	21	24
8	f	42	58	0	24
18	f	43	57	0	7
1	f	90	0	10	10
4	m	92	3	5	59
9	m	37	0	63	19
14	m	50	8	43	40
6	m	86	14	0	64
2	m	85	0	15	13
34	m	56	0	44	36
19	m	67	33	0	6
11	m	82	9	9	11

Table 4.6. Dry matter composition of winter porcupine food, including white spruce needles (n = 8), paper birch cambium (n = 1), and white spruce cambium (n = 2) in Anchorage, Alaska.

	White Spruce Needles	Birch Cambium	White Spruce Cambium
g N/100 g DM	1.075 ± 0.126	0.999	0.808 ± 0.007
g C/100 g DM	50.832 ± 0.507	48.321	50.426 ± 2.048
g NDF/g DM	0.532 ± 0.025		
mmol Phenols/100 g DM	0.508 ± 0.235	12.860	8.036 ± 2.675

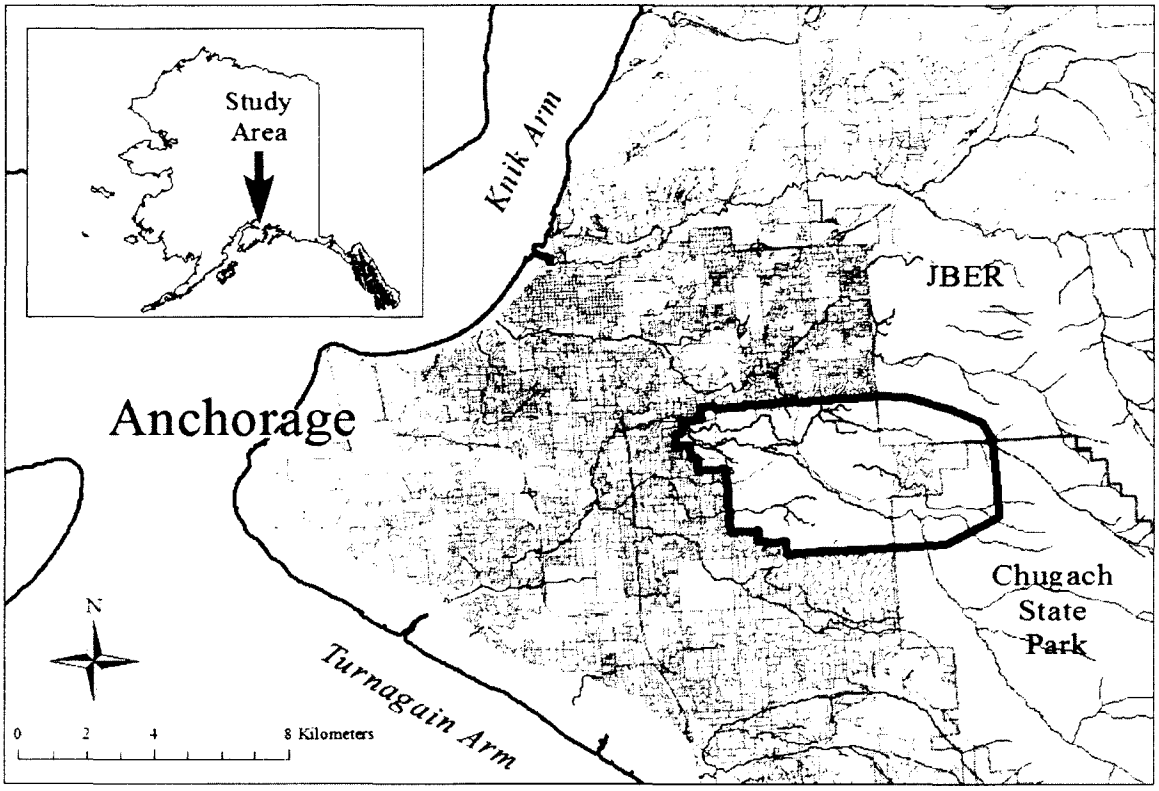

Figure 4.1. Location of study area (37 km2) in Anchorage, Alaska.

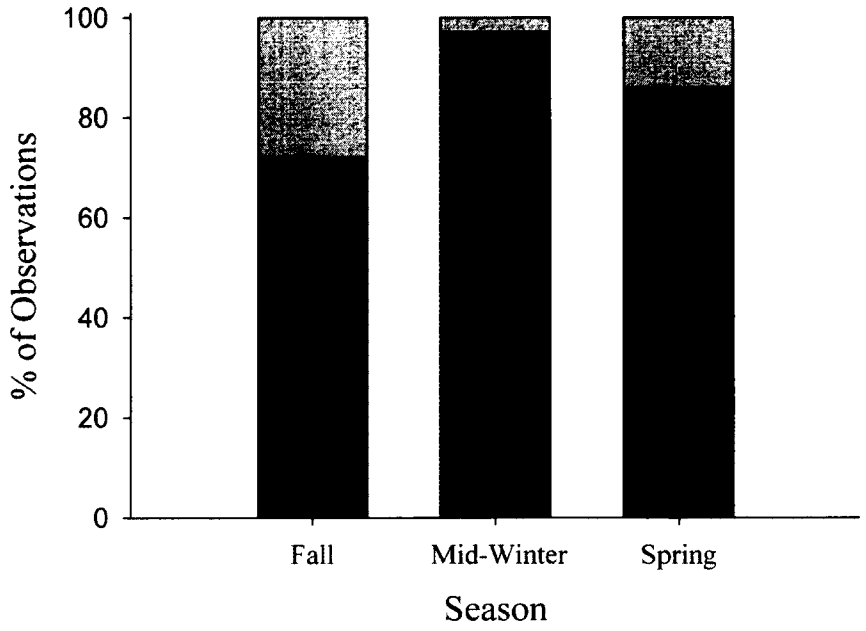

Figure 4.2. Frequency of porcupines observations in white spruce (black), paper birch (dark grey) and cottonwood (light grey) trees during fall (n = 42), mid-winter (n = 318), and spring (n = 74) in Anchorage, Alaska (2005-2008).

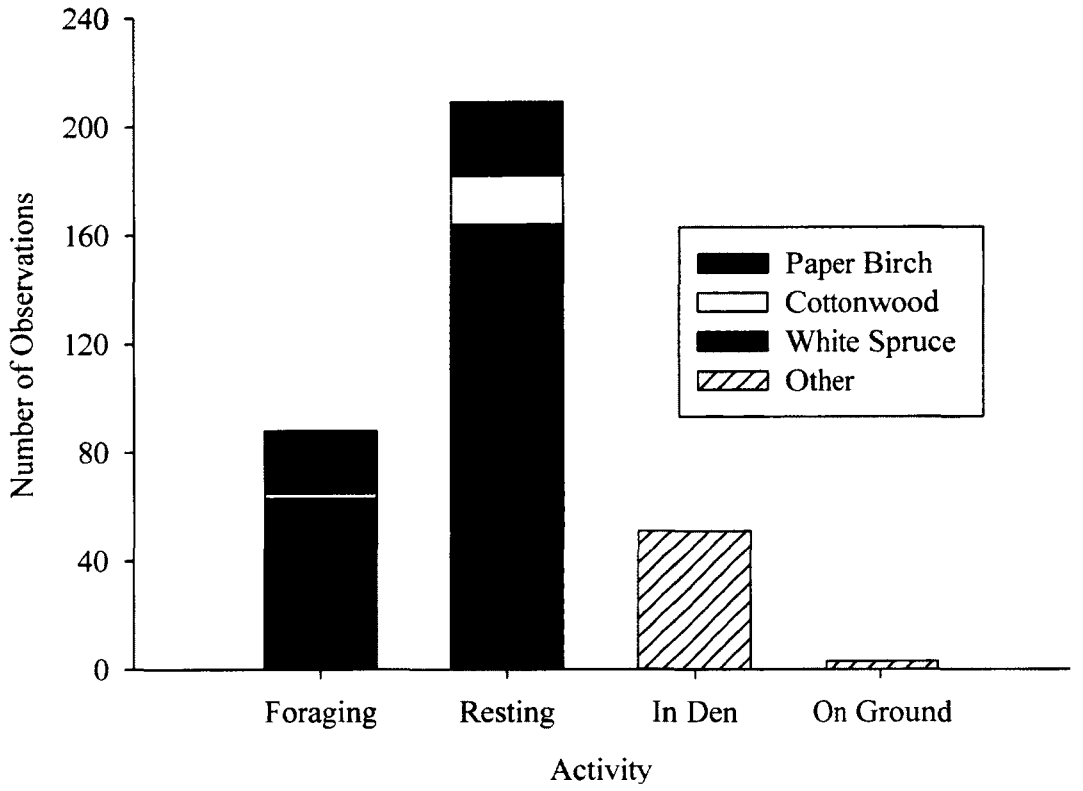

Figure 4.3. Visual observations of porcupines (n = 19) in Anchorage, Alaska during the winters of 2005-2006, 2006-2007, and 2007-2008. A total of 363 observations of porcupine activity are included in this figure.

CHAPTER 5 – CONCLUSION

Introduction

This study was the first to examine the physiology and ecology of porcupines during the extreme environmental conditions of an Alaskan winter. My objectives were: 1) to identify the physiological ability of porcupines that enable them to survive on low quality winter forage, 2) to determine responses of porcupines to winter conditions, and 3) to determine how winter conditions influence habitat selection and home range size at the northern limits of their geographic range.

Nutritional Constraints of Winter

In **CHAPTER 2,** I used captive porcupines to examine physiological responses to low quality diets, a formulated ration and white spruce (*Picea glauca*) needles, at ambient temperatures as low as -39 °C. Captive porcupines were able to maintain body mass over winter when provided the formulated ration lacking plant secondary metabolites (PSM; Figure 2.1), even though other studies have shown that wild porcupines tend to lose 30-40 % body mass throughout the winter season (Berteaux et al. 2005; Oveson 1983; Roze 1984; Smith 1979; Sweitzer and Berger 1993; Tenneson and Oring 1985). These results indicate that porcupines can utilize higher quality food resources opportunistically to compensate for loss in body mass. A flexible response to quality of food may have contributed to the wide geographic distribution of porcupines throughout North America.

While an endogenous pattern of body mass regulation was not evident in captive porcupines fed *ad libitum*, these animals reduced dry matter intake (DMI) during winter (Figure 2.2). Porcupines that consumed the formulated diet throughout the winter decreased DMI from 43.62 ± 12.73 g · $kg^{-0.75}$ · d^{-1} in early winter to 14.58 ± 2.06 g · $kg^{-0.75}$ · d^{-1} in late winter without a change in digestibility of DM (Figure 2.2). Declines in DMI over winter were unexpected, because the corresponding decline in ambient temperature (Figure 2.1) typically results in increased thermoregulatory costs (Wunder 1975, 1992). Although digestible DMI declined (Figure 2.2), porcupines were able to

maintain body mass as ambient temperatures fell, which suggests that porcupines can decrease metabolic costs as winter progresses. Energy intakes of porcupines on the formulated ration decreased from 625 ± 137 kJ · $kg^{-0.75}$ · d^{-1} to 256 ± 36 kJ · $kg^{-0.75}$ · d^{-1} of gross energy and from 562 ± 172 kJ · $kg^{-0.75}$ · d^{-1} to 193 ± 33 kJ · $kg^{-0.75}$ · d^{-1} of digestible energy between early winter and late winter.

On average, the maintenance energy requirement estimated for porcupines (398 kJ · $kg^{-0.75}$ · d^{-1}) was similar to that estimated for other arboreal folivores (Nagy and Montgomery 1980; Ullrey et al. 1981) and lower than those of other eutherian mammals including smaller bodied rodents with active lifestyles, such as species in the genus *Microtus* (Hayssen and Lacy 1985). The low maintenance energy requirements observed in porcupines suggests a low basal metabolic rate (BMR) with a potentially lower critical temperature (LCT) for increasing energy expended on thermoregulation.

High phenol concentration in white spruce needles (Table 2.1) corresponded with decreased DMI in porcupines; porcupines fed white spruce needles exhibited a more pronounced decline in digestible DMI compared to animals fed the formulated diet (70 % vs. 43 % decline) between mid- and late winter (Table 2.3). Although porcupines maintained similar digestible intakes of energy from the formulated diet and white spruce needles, less energy was retained from the white spruce needles (up to 42 % less MEI; Table 2.4). While this study did not specifically explore detoxification pathways, 20 to 21 % of digestible energy intake was lost via urine when porcupines were fed white spruce needles. Most likely a large portion of this urinary energy loss can be attributed to detoxification of PSM. Porcupines may reduce consumption of forages with high levels of PSM as detoxification pathways become saturated.

Porcupines were able to maintain nitrogen (N) balance on the formulated ration, at only 1.1 % N in dietary DM. True nitrogen digestibility was high for both diets (98 ± 1 % for formulated ration and 97 ± 2 % for white spruce needles). My estimates of N requirements for porcupines during mid- and late winter in Alaska (209 ± 92 mg · $kg^{-0.75}$ · d^{-1}) were lower than those derived by both Felicetti et al. (2000; 346 mg · $kg^{-0.75}$ · d^{-1}) and Fournier and Thomas (1997; 389 mg · $kg^{-0.75}$·d^{-1}) and much lower than the mean for other

eutherian herbivores (582 ± 235 $mg \cdot kg^{-0.75} d^{-1}$; Robbins 1993; Figure 2.5). The majority of urinary N was probably associated with excretion of conjugated PSM, because only 20 % of urinary N was attributed to urea N in porcupines fed white spruce needles. In late winter, we found that porcupines maintained zero N balance while consuming white spruce needles. These results suggest that the cost of detoxifying and eliminating PSM exceeds digestible N intake because dietary N content is low, food intake is depressed, and N is lost to processing PSM.

There was no indication that either water balance or acid base balance was affected by consumption of white spruce needles since osmotic concentrations of urine relative to plasma (U/P ratio) and urinary pH were similar among experimental periods and between diets. While it is possible that PSM in white spruce may increase water intake in porcupines, these data indicate that consumption of snow was sufficient to maintain water and acid base balance. Furthermore, sodium (Na) balance of porcupines was not significantly different from zero. Therefore, wintering porcupines probably require significantly less Na than most mammals (10 $mg \cdot kg^{-1} \cdot d^{-1}$; Robbins 1993).

The results of **CHAPTER 2** suggest that during winter in Alaska, nutrition may ultimately dictate survivorship and influence the size of local populations of porcupines. Available winter forage poses additional physiological challenges due to high PSM content, low energy content, and imbalanced mineral content, while low ambient temperatures increase thermoregulatory demands. Porcupines may switch between dietary items to increase intake by varying detoxification pathways for different PSM (Dearing et al. 2005b; Freeland and Janzen 1974) and by alleviating imbalances in mineral intake. Regardless, by the end of winter, porcupines display multiple imbalances in energy, N, and several minerals, that are only alleviated by the consumption of spring forages.

Responses to Winter

In **CHAPTER 3**, I examined the ability of porcupines to conserve lean body mass through seven months of winter in Alaska by measuring body composition and by

estimating energy expenditure of captive and free-ranging wild porcupines. I found that free-ranging porcupines exhibit a seasonal variation of body mass and composition that is not apparent in captive porcupines maintained under similar environmental conditions, including similar ambient temperatures and artificial den structures (**CHAPTER 2**). The seasonal variation in body mass in free-ranging porcupines is associated primarily with changes in fat mass, as lean mass remains relatively constant year round (Table 3.1). Peak fat mass is obtained at the onset of a seasonal decline in food quality, and the use of fat stores coincides with a dietary shift to winter forages that are low in digestible energy and high in PSM. Porcupines probably reach their lowest fat mass in late spring (late May) because fat was still 27 % of body mass at the time of the spring collection period (March - April), which preceded the emergence of spring vegetation by 3-4 weeks. Therefore, fat reserves probably were necessary to meet daily energy requirements for at least another month beyond when porcupines were sampled.

Unlike most northern herbivores, porcupines maintain lean mass over the winter (Adamczewski et al. 1997; Barboza and Parker 2008; Dark and Zucker 1983; Holand 1992; Parker et al. 1993; Voltura 1997; Table 2.1). This result was unexpected, as winter diet is low in N and energy **(CHAPTER 2)** when thermoregulatory costs are high. Porcupines probably maintain lean mass by combining low N requirements with an ability to spare body protein while using large fat stores (Barboza et al. 2009). It is possible that to survive winter porcupines with insufficient fat reserves might be forced to catabolize body protein as the season progresses. The rate of winter mass loss for individual porcupines was not affected by their initial lean mass but depended on the amount of fat they possessed in the fall (Figure 3.3). Although adult free-ranging male porcupines were larger than adult free-ranging females in the fall, there was no difference between the sexes in the proportion of body mass that was fat. Therefore, due to sexual dimorphism in porcupines, males lose absolutely more fat than females, but the proportion of body mass lost as fat is similar between the sexes.

I did not find any evidence that porcupines reduce metabolic costs by lowering core body temperature on a daily or seasonal basis (Fig. 3.4); core body temperatures

varied by only 1.5 °C daily. Therefore, porcupines must rely on behavioral and other physiological adaptations to conserve fat stores and still meet high thermoregulatory demands in winter (DeMatteo and Harlow 1997; Oveson 1983; Po-Chedley and Shadle 1955; Roze 1987). It is probable that porcupines in the northern limits of their range are acclimatized to a LCT < -2 °C, as estimated by DeMatteo and Harlolw (1997), because porcupines in this study were subjected to >100 days of ambient temperatures < -11 °C. Maintaining a LCT < -2 °C would allow for additional thermoregulatory savings.

Water turnover rates for both captive and free-ranging porcupines are extremely low compared to the mean for eutherian mammals (123 ml· kg^{-80} · d^{-1}; Richmond et al. 1962; Table 3.2). However, water turnover rates based on lean mass of porcupines are similar to whole body turnover rates for other arboreal folivores that are typically lean and store little fat (Degabriel et al. 1978; Kennedy and Heinsohn 1974; Krockenberger 1993; Nagy and Montgomery 1980). Low turnover rates in porcupines are both a reflection of water availability and use (Degabriel et al. 1978). We saw no evidence that captive porcupines with significant water turnover rates were in osmotic stress based on osmotic concentrations of urine relative to plasma (U/P ratio; **CHAPTER 2**). Production of metabolic water most likely plays an important role in water balance because oxidation of fat stores produces 1.07 g H_2O · g^{-1} fat. In free-ranging porcupines, daily fat loss of 12.78 ± 4.97 g · d^{-1} would produce 13.67 ± 5.32 g H_2O · d^{-1}, or 52 % of daily water turnover.

Estimated field metabolic rate (FMR) for free-ranging porcupines was low compared to other eutherian herbivores (Table 3.3; Nagy et al. 1999). On a lean mass basis, FMR was 4.4 times the predicted basal metabolic rate based on body size (Kleiber 1947), and only 31 % lower than predicted FMR based on whole body mass (4,130 ± 613 kJ · $kg^{-0.734}$ · d^{-1}; Nagy et al. 1999). The lower than predicted FMR for porcupines is most likely influenced by diet selection and thermoregulatory capacity (Nagy et al. 1999).

Porcupines conserve lean body mass in winter by balancing the consumption of poor-quality forages with the use of fat stores. Fat losses are minimized by lowering rates of energy expenditure (i.e., FMR) and water turnover. While porcupines

can use a wide variety of diets across their broad geographic distribution, winter survival is dependent on food quality at the northern limits of their range. During winter, porcupines function as dietary specialists consuming forage high in PSM. However, this strategy is not sustainable year round, because animals must replenish their stores of fat and protein for survival and reproduction in the following year. As a result, porcupines must switch to a generalist strategy with the arrival of spring forage (**CHAPTER 1**).

Habitat Selection and Home Range Size

I tracked free-ranging porcupines over three winters in south central Alaska to determine habitat selection and home range size in relation to diet (**CHAPTER 4**). My estimates of home range size (0.98 ± 0.33 km^2, 95 % isopleth KDE and 1.71 ±2.30 km^2, MCP) were larger than those reported for porcupines in more temperate habitats (Craig and Keller 1986; Zimmerling and Croft 2001). The relatively large home ranges in southcentral Alaska are most likely a result of patchy distribution of preferred forage or roost trees, low availability of den sites, low predation risk and larger body size of Alaskan porcupines compared to those at lower latitudes (Roze 2009; Sweitzer and Berger 1993). Understanding site specific daily movement rates for individual porcupines would help increase the accuracy of home range estimates.

While I did not find any specific selection for mixed forest types, porcupines selected against some habitats dominated by single species, including barren, black spruce (*Picea mariana*), shrub (*Betulaceae spp.*), and white spruce (Table 4.3). A comparison among all habitat types indicated that porcupines selected mixed conifer/hardwood forests over black spruce, bluejoint meadow and shrub habitats. The weak relationship observed between white spruce and mixed conifer/hardwood forest is most likely a result of low relocation numbers for some individual porcupines. However the use of mixed forests over white spruce dominated forests suggests that white spruce alone may not satisfy winter nutritional requirements of porcupines, regardless of the thermoregulatory benefits of coniferous trees.

Variation in tree use among individual porcupines was large and this resulted in a inability to ascertain any statistically relevant pattern of microhabitat selection in our study area. However, direct observations revealed that porcupines used two forage tree species (paper birch and white spruce) during winter, and most observations of porcupines were in white spruce trees. It is possible that white spruce needles may have provided a slight nutritional advantage over paper birch, since white spruce needles were higher in nitrogen and lower in total phenols than other dietary items. However, my nutritional analysis was limited, and I recommend additional component analyses to better understand the role of nutrition in habitat selection. The use of white spruce as forage and roosting trees may have provided a higher thermoregulatory advantage over paper birch trees (Clarke and Brander 1973; Roze 2009). Den use was infrequent in our study area and did not appear to be related to porcupine size or ambient temperature. White spruce trees may provide refugia for Alaskan porcupines that is similar to the thermal refugia provided by dens for porcupines in other locations.

Regardless of potential nutritional or thermoregulatory advantages provided by white spruce trees, porcupines were frequently observed in paper birch trees during winter. Since deciduous trees should not provide a thermal advantage during winter, it is likely that a nutritional requirement is met by paper birch cambium. Switching to a diet of paper birch cambium may allow porcupines to increase intake by varying detoxification pathways for different plant secondary metabolites (Dearing et al. 2005a; Freeland and Janzen 1974).

My data indicate that porcupines maintain large winter home ranges that are dominated by mixed conifer/hardwood forests in southcentral Alaska and avoid homogenous stands of deciduous or hardwood trees, which are typically targeted for commercial harvest. However, porcupines are incredibly adaptable herbivores, as demonstrated by the wide array of habitats that they occupy throughout North America, as well as by recent northward and southward range expansions (Ilse and Hellgren 2001; Payette 1987; Spencer 1964). Their ability to occupy novel habitats suggests that porcupines may be able to expand to single species stands in southcentral Alaska if

preferred mixed conifer/hardwood stands are unavailable. Maintaining mixed forests would provide suitable winter habitat for porcupines and may alleviate damage to single species stands of conifers or hardwoods that are preferred by commercial forestry operations.

Implications

While the porcupine is one of the most widespread herbivores in North America (Dodge 1982), surprisingly few studies have explored the ecology and physiology of this adaptable rodent. My research describes physiological abilities unique in North American rodents. Unlike many northern mammals, porcupines evolved in South America and migrated north across the land bridge between the two continents (Vilela et al. 2009; Woods 1973). This evolutionary pathway may have helped porcupines evolve the physiological plasticity that enables them to persist on dietary items that are not used by other mammals, as well as the ability to gain body mass when the abundance and quality of food permits (**CHAPTER 2**; Coltrane and Barboza 2010). These characteristics distinguish porcupines from other herbivorous northern mammals and make porcupines an extraordinarily successful species in a variety of habitats.

Ironically, it is this adaptability that has led to their characterization as generalist herbivores (Dodge 1982). My data add to the body of literature which indicates that the porcupine exhibits dietary specialization on a regional, temporal, and individual basis. Therefore I recommend that porcupines be reclassified as facultative dietary specialist, as described by Shipley et al. (2009; **CHAPTER 1**). However, I recommend additional research to better define the degree of specialization exhibited by porcupines throughout their range. Comparative studies of diet selection across habitats will provide insight into regional and seasonal dietary specialization. Captive studies are required to understand the physiological mechanisms used by porcupines to consume difficult foods, specifically metabolic pathways used to process PSM found in local plants. Furthermore, documenting inter-population and individual differences in the ability to metabolize PSM will provide insight into the ecology and evolution of porcupines, which

may ultimately explain habitat selection, dispersal and gene flow (Mangione et al. 2000) of porcupines.

The dietary versatility of the porcupine as a facultative specialist is demonstrated by both northward and southward range expansions (Ilse and Hellgren 2001; Payette 1987; Spencer 1964). Distributional changes may have significant impacts on ecosystems, especially on rare species (Alverson et al. 1988). Understanding the physiological and morphological ability of porcupines to specialize on novel diets will assist in predicting and managing impacts of populations as they expand and establish in new areas.

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